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NUTRITIONAL STUDIES BY MEANS OF TISSUE TESTS WITH POTATOES GROWN ON A MUCK SOIL[1]

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INTRODUCTION

Innumerable field fertilizer experiments, in which yield was employed as the evaluating factor, have failed to provide reliable fundamental information which might be applied to fertilizing specific crops over a range of soils and climate. The addition to the soil of a fertilizer in amounts assumed to be adequate is no assurance that the nutrient is effectively entering the plant and many experiments have failed to give true information due to such an assumption.

Considerable progress has been made in the use of plant analyses in diagnosing mineral deficiencies and in determining nutrient requirements. The concentration of a nutrient in a plant is a function of many factors such as soil, climate, fertilizer applications, etc., and it is just this sensitivity of the plant to its environment that makes plant analyses of value. The development of rapid semi-quantitative chemical tissue tests has made possible a nutritional survey of relatively large areas in a short time at low cost. It may be possible to establish critical concentrations for each nutrient for individual crops by making many observations in which yields are compared to analytical values. Present studies had the object of establishing critical nutrient concentrations of the potato plant at one stage of growth.

MATERIAL AND METHODS

The present studies were conducted on a deep organic muck soil, the average organic matter content ranging from 80 to 85 per cent and the well decomposed layer extending to an average depth of fourteen inches. The soil is slightly acid in reaction (pH 5.6 to 6.5) and potash and phosphoric acid are deficient in the virgin muck. The fertilizer plots from which this material was collected were laid down in 1937, the plots being outlined with permanent markers. Each plot area has received the same fertilizer each year the experiment has been conducted.

The plots were arranged as a factorial experiment involving three levels of nitrogen 0, 30 and 60 pounds per acre, three levels of phosphoric acid and potash 0, 120 and 240 pounds per acre, involving twenty-seven plots in each of three randomized blocks. Each plot consisted of five rows, twenty-five feet long. Records were taken from three rows, twenty-one feet long, or from an area of 1/230 acre.

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Certified seed tubers of Green Mountain potatoes were employed each year.

Samples of petioles were selected from each plot in two blocks in 1944 to 1946, inclusive. Petioles from the lower third portion of the plant were taken for analysis from twelve different plants selected at random in different sections of the plot. Samples were taken at only one stage of growth, approximately six to seven weeks after planting. Hawkins (6) found that the Green Mountain variety absorbed about 70 per cent of its total consumption of plant nutrients during the season, between fifty and eighty days after planting, so it was considered that at the time of sampling plant nutrient demand would be close to the maximum.

Chemical Methods

A five gram green weight sample of petiole tissue was extracted with 50 ml. of 2 per cent acetic acid in a Waring Blendor, a small amount of charcoal (Darco G 60) being added to produce a colourless solution upon filtration.

The levels of the different elements were determined on aliquots of this filtrate, employing a Klett-Summerson colorimeter to evaluate colour intensities against those obtained with a range of standards. Soluble nitrogen and phosphorus were determined on a one or two ml. aliquot according to the methods used by Emmert (4) and Carolus (2). Potassium was determined by the method of Garman (5) as modified by Johnstone and Myles (7). Calcium and magnesium were determined by the methods of Peech and English (9). In calculating results the aliquot of the filtrate employed for a test was considered as a fraction of the extracting solution used, so that 10 cc. of filtrate represented one gram of plant tissue. Carolus (2) on the other hand considered the aliquot of the filtrate employed as a fraction of the extracting solution plus the weight of sample, so that, comparatively, the results reported are but five-sixths of the values if his method of calculation had been used.

In order to express the relationships between yields and the amounts of the different elements contained in leaf tissues and the inter-relationships between the concentration of the elements themselves, use has been made of the simple partial and multiple correlation coefficients. These coefficients have all been calculated by present standard methods and the usual tests of significance applied in each case. To determine the relationships existing in both "low" and "high" ranges of the various elements, the data were assembled in ascending order of the concentration of each element under consideration. The point at which the whole range was split into the two groups or sub-ranges was determined by visual inspection of scatter diagrams showing the relationship between yield and the amounts of each individual element.

RESULTS, 1944

The parts per million of soluble nitrogen, phosphorus and potassium found in the tissues, along with fertilizer treatments, yields and growth observations, are found in Table 1. An examination of the data reveals that in some cases large differences exist in yields, growth observations and levels of constituents in the plant tissue between duplicate plots receiving

TABLE 1

Fertilizer formula	Parts per million			Yield	Growth notes	Parts per million			Yield	Growth notes
	N	P	K			N	P	K		
0-0-0	154	56	2917	95.5	Foliage dark green, vigour good.	31	87	3678	81.0	Foliage light green, vigour medium.
0-0-8	280	4	4606	92.0	Foliage normal colour, vigour medium.	29	79	3929	101.0	Foliage light green, vigour fair.
0-0-16	30	54	3318	89.5	Foliage light green, medium vigour.	44	34	12309	88.0	Foliage light green, only medium vigour.
0-8-0	586	118	—	28.5	Dwarfed, foliage dark green, scorched.	51	51.6	2390	56.0	Foliage light green, spindly, med. vigour.
0-8-8	57	85	4606	86.5	Foliage medium colour, vigour medium.	43	84.0	4166	84.0	
0-8-16	21	34	3839	107.0	Foliage light green, vigour fairly good.	31	64.0	3333	95.0	Foliage light green, medium vigour.
0-16-0	15	83	4201	108.5	Foliage light green, medium vigour.	21	59.0	3676	94.0	Foliage light green.
0-16-8	91	57	4606	87.0	Foliage medium green, vigour fairly good.	181	128.0	4292	94.5	Normal colour, good vigour.
0-16-16	43	53	4724	75.5		50	53.0	3181	84.0	
2-0-0	76	47	480	38.0		21	36.0	4824	97.0	
2-0-8	—	61	—	71.0	Vigour fair, foliage normal.	513	—	4934	90.0	Foliage dull dark green, vigour medium.
2-0-16	166	22	4203	101.5	Vigour good, foliage normal	195	39.0	3836	94.0	Foliage normal, good vigour.
2-8-0	418	135	3929	65.0	Foliage normal green, vigour fair.	55	79.0	2362	61.5	Foliage normal, vigour fair.
2-8-8	32	55	3051	70.0	Foliage light green, vigour medium.	37	61.0	4403	84.0	
2-8-16	55	52	4472	116.5	Foliage medium colour, vigour medium.	55	80.0	4093	93.0	Foliage slightly light green.
2-16-0	150	94	1897	66.0	Foliage dull dark green, vigour medium.	239	106.0	869	59.5	Vigour only medium to fair.
2-16-8	168	56	2731	82.5	Foliage normal, medium vigour.	106	70.8	5401	104.0	Good vigour.
2-16-16	70	51	4204	85.5	Foliage light green, medium vigour.	116	62.0	5569	106.5	Foliage normal, good vigour.
4-0-0	248	19	982	68.0	Foliage dull dark green, medium vigour.	812	145.0	210	42.0	Scorching of foliage, vigour reduced.
4-0-8	369	29	3676	90.0	Foliage normal, vigour good.	200	38.0	4924	92.0	
4-0-16	111	50	4472	87.0	Foliage normal, vigour medium.	120	63.0	4425	102.0	Foliage normal, vigour good.
4-8-0	414	142	643	43.5	Foliage scorched, vigour reduced.	748	193.0	889	42.5	Foliage dark green, scorched, vigour reduced.
4-8-8	451	42	4427	83.0	Good vigour.	239	67.0	4502	83.0	Foliage normal, vigour good.
4-8-16	460	24	3676	79.5	Foliage normal, vigour fair.	232	73.0	3530	82.5	Foliage normal, good vigour.
4-16-0	404	146	3929	80.0	Slightly dwarfed, foliage normal.	601	286.0	93	43.0	Scorching severely reduced in vigour.
4-16-8	181	118	2666	74.5		184	39.0	4080	89.0	Foliage normal, vigour good.
4-16-16	192	84	5329	81.0	Foliage normal, good vigour.	426	107.0	341	61.0	Scorching severe, vigour reduced.

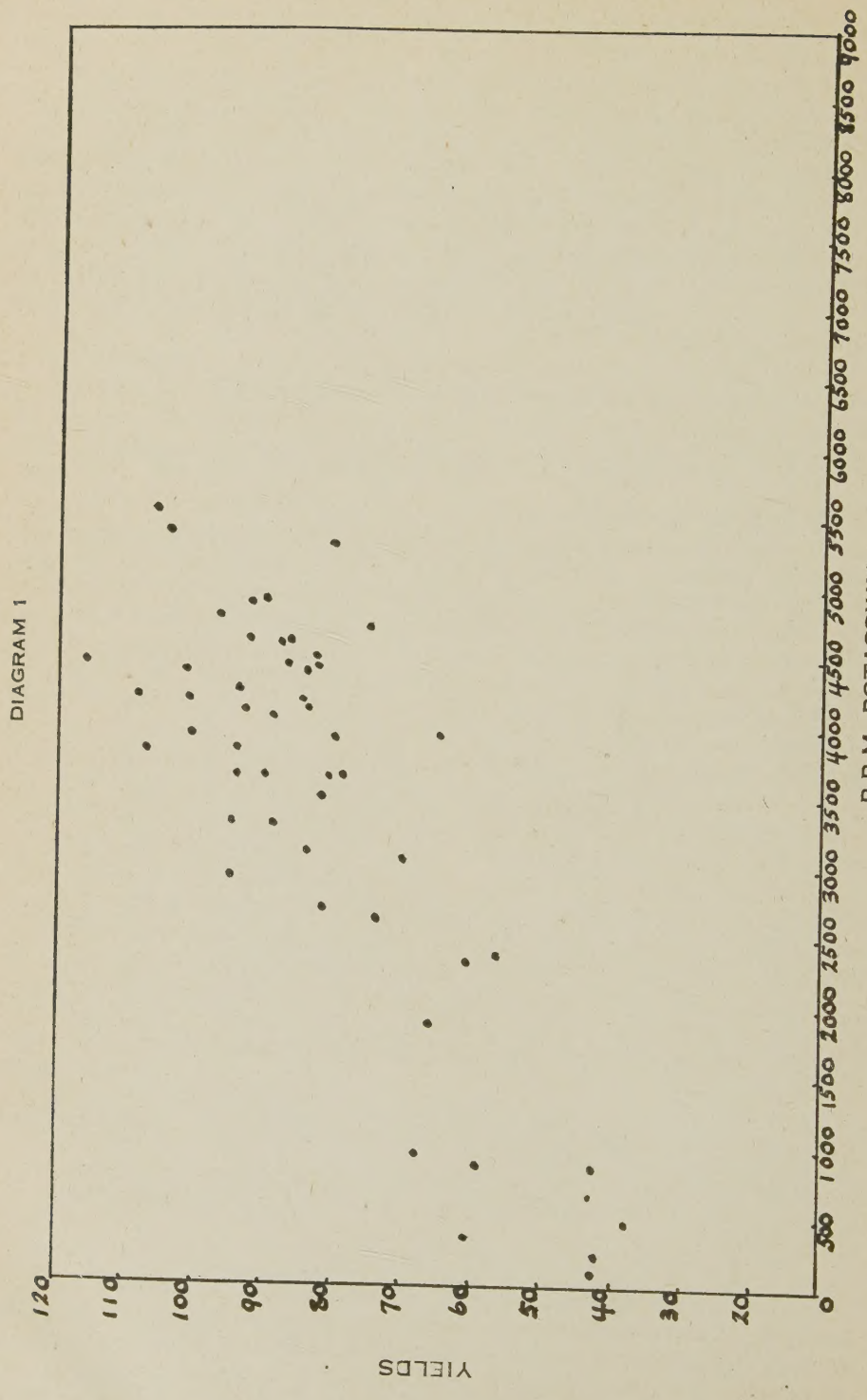


DIAGRAM 1
YIELDS
120
110
100
90
80
70
60
50
40
30
20
0
500
1000
1500
2000
2500
3000
3500
4000
4500
5000
5500
6000
6500
7000
7500
8000
8500
9000
P.P.M. POTASSIUM

the same fertilizer treatments. In this regard it may be stated that the land occupied by these plots was subjected to partial flooding in the spring, which may well account for such differences. Differences between duplicate plots are especially large in the following treatments:—0-8-0; 2-0-0; 4-0-0; 4-16-0; and 4-16-16. Such large differences in yields between duplicate plots make it difficult to correctly interpret the effect of fertilizer treatment on yield, but the tissue analyses reveal the reason for such large yield differences. It will be observed that the lower yield in each plot of a pair of duplicates is associated with a considerably reduced level of potassium in the tissues.

While details are not herein included statistical analysis of the entire experiment showed no significant increases in yields due to the application of either nitrogen or phosphoric acid but that significant increases in yield were obtained by applications of potash; applications of 240 pounds per acre not significantly increasing yields over those obtained with applications of 120 pounds per acre.

Relationship between Levels of Potassium in the Plant Tissues and Yields

The relationship between levels of potassium in the plant tissues and yields is shown by Spot Diagram 1. There is a positive correlation over the entire range (phosphorus and nitrogen effects accounted for) between the levels of potassium in the tissues and yields ($r = + .356$).

With levels of 4000 p.p.m. and above, relationship with yields is not significant ($r = - .266$); while if levels are below 4000 p.p.m. there is a high positive correlation ($r = + .717$).

Relationship between Levels of Phosphorus in the Plant Tissues and Yields

This simple relationship is shown by means of Spot Diagram 2. The simple correlation shows a significant negative relationship between levels of phosphorus in the tissues and yields ($r = - .548$), but when nitrogen and potassium effects are accounted for the relationship is not quite significant ($r = - .313$).

There appears to be a change in relationship between the lower and higher levels of phosphorus and yields. From the lowest level of phosphorus up to 70 p.p.m. there is no significant correlation ($r = + .046$). With levels of phosphorus above 70 p.p.m., nitrogen and potassium effects being accounted for, the apparent negative relationship just falls short of being significant ($r = - .374$).

Relationship between Levels of Nitrogen in the Plant Tissues and Yields

There is a simple negative relationship between levels of nitrogen in the plant tissues and yields ($r = - .552$), and this relationship still exists after effects of phosphorus and potassium have been accounted for ($r = - .441$).

When the nitrogen levels are divided into two categories 15-200, and 200-900 p.p.m., the following relationships are shown. With a range of nitrogen up to 200 p.p.m. there is no relationship ($r = + .056$), but with levels from 200-900 p.p.m. there is a significant negative relationship between nitrogen and yields ($r = - .613$).

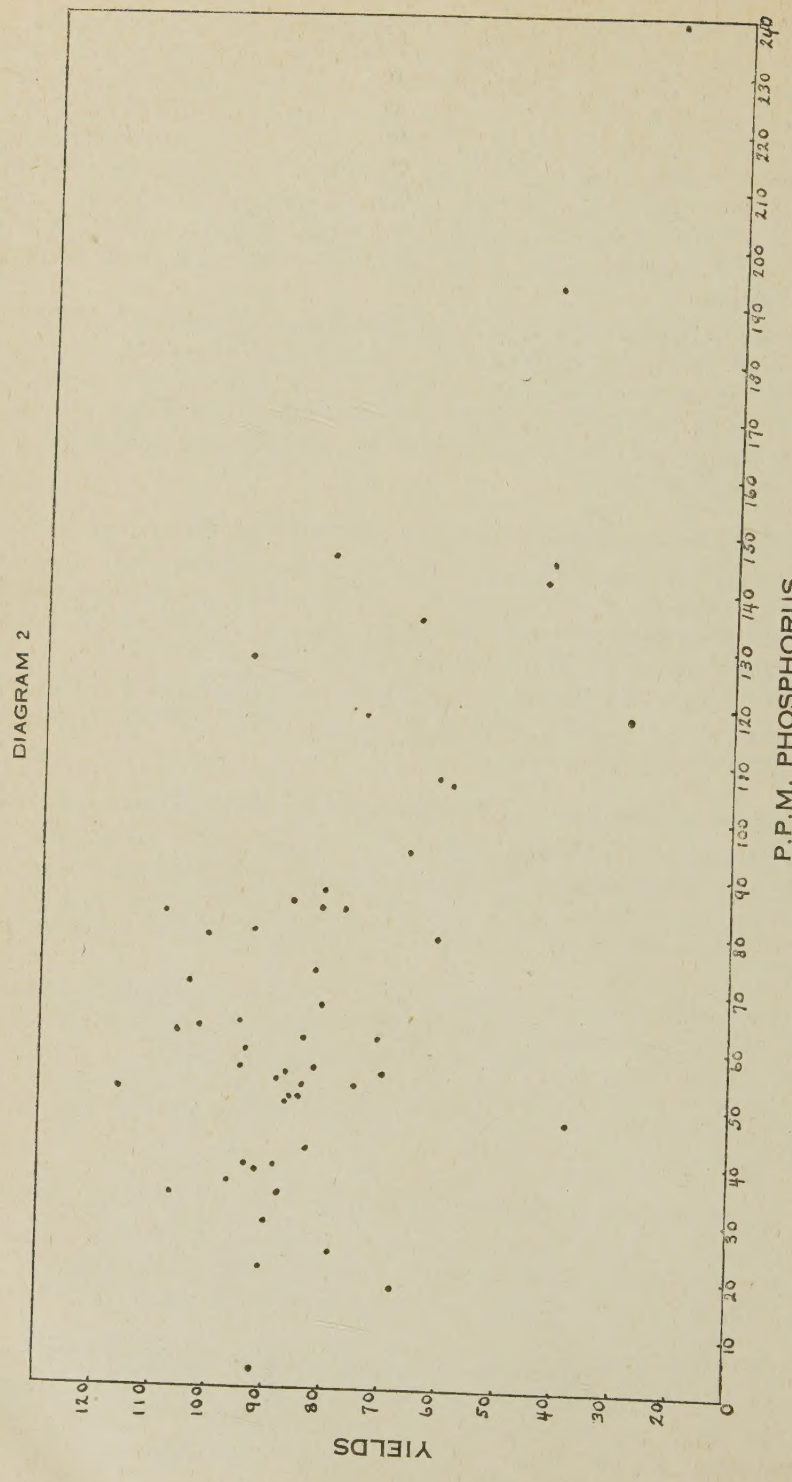


DIAGRAM 2
YIELDS
P.P.M. PHOSPHORUS
0
10
20
30
40
50
60
70
80
90
100
110
120
130
140
150
160
170
180
190
200
210
220
230
240
20
30
40
50
60
70
80
90
100
110
120

However, in the majority of cases of high nitrogen and low yields phosphorus is also at a high level and potassium at a low level. With potassium accounted for there is a positive relationship between nitrogen and phosphorus ($r = + .435$); that is, nitrogen and phosphorus increase together. With phosphorus accounted for there is no relationship between nitrogen and potassium ($r = - .159$) and with nitrogen accounted for there is no significant relationship between phosphorus and potassium ($r = - .251$).

There is, however, a significant relationship between the combined unit of nitrogen and phosphorus on potassium ($R = .403$). It is therefore questionable whether there is a direct relationship between high nitrogen and low yield, or between high phosphorus and low yield. It would appear to be rather a joint effect of high nitrogen and high phosphorus bringing about a reduction of the potassium content.

RESULTS, 1945

The parts per million of soluble nitrogen, phosphorus and potassium found in the tissues along with fertilizer treatments, yields and growth observations are shown in Table 2. The early part of the season was one of abnormally high precipitation and the foliage of many plots was yellowish-green reflecting the saturated conditions of the soil with probably poor soil aeration conditions. The average yield was somewhat lower than in 1944.

Relationship between Fertilizers Applied and Levels Found in the Plant Tissues

The application of potassium is generally reflected in increased potassium in the tissues. The average level of potassium in the tissues for all plots not receiving potassium is 1107 p.p.m. and the average yield 37.9; for plots receiving 8 units in the formula or 120 lbs. of K_2O per acre the average level is 3551 p.p.m. and the average yield 81.7 and for all plots receiving 16 units or 240 lbs. of K_2O per acre the average level is 4887 and the average yield 88.7.

The application of phosphorus only is reflected in increased phosphorus in the tissue and a reduction of potassium but when applied along with potassium the phosphorus levels are not increased.

The application of nitrogen is reflected in increased nitrogen in the tissues. The average level of nitrogen in the tissues for all plots not receiving nitrogen is 88 p.p.m.; for plots receiving 2 units or 30 lbs. of nitrogen per acre the average level is 233 p.p.m. and for all plots receiving 4 units or 60 lbs. of nitrogen per acre the average level is 334 p.p.m.

Relationship between Levels of Potassium in the Plant Tissues and Yields

When the effects of nitrogen and phosphorus are accounted for there is a positive correlation over the total range between potassium in the tissues and yields ($r = + .644$).

With levels of 4000 p.p.m. and above relationship with yields is not significant ($r = - .163$), while with levels below 3000 p.p.m. there is a high positive correlation ($r = + .753$).

TABLE 2

Fertilizer formula	Parts per million N	P	K	Yield	Growth notes
BLOCK I					
0-0-0	63	195	1300	45.1	Reduced in vigour, slight scorching.
0-0-8	83	120	3420	71.5	Foliage light green, only med. vigour.
0-0-16	150	120	3140	83.5	Foliage lightish green.
0-8-0	145	340	700	24.7	Dwarfed, lacking vigour, scorching severe.
0-8-8	50	180	3620	52.2	Foliage quite light green, vigour poor.
0-8-16	43	160	2160	89.3	Foliage light green, med. vigour.
0-16-0	225	340	650	27.9	Lacking vigour, dwarfed, scorch severe.
0-16-8	40	198	2640	81.3	Foliage light green, vigour medium.
0-16-16	60	170	5264	65.6	Foliage light green, vigour reduced.
2-0-0	180	210	1310	45.3	Dwarfed, medium scorching, vigour reduced.
2-0-8	150	130	3130	93.6	Foliage slightly light green, medium vigour.
2-0-16	230	234	3140	80.6	Normal colour, medium vigour.
2-8-0	525	270	585	29.0	Dwarfing, severe scorch.
2-8-8	135	146	1850	82.2	Foliage slightly light green, med. vigour.
2-8-16	135	190	3150	95.5	Normal colour, vigour good.
2-16-0	355	310	650	41.4	Severe scorch, medium vigour.
2-16-16	238	310	6580	97.6	Good vigour, well branched.
2-16-8	230	194	3600	92.1	Normal colour, good vigour.
4-0-0	600	245	300	26.2	Dwarfed, severe scorch.
4-0-8	155	46	5240	97.6	Normal colour, good growth.
4-0-16	—	—	—	—	
4-8-0	730	440	2360	27.9	Severe scorch, dwarfed.
4-8-8	240	130	3400	83.1	Colour normal, medium vigour.
4-8-16	350	265	8940	102.4	Foliage normal, good vigour.
4-16-0	1000	370	1580	46.3	Severe scorch, dwarfed.
4-16-8	90	182	—	99.6	Foliage slightly light green, good vigour.
4-16-16	375	210	4460	99.8	Foliage normal, well-branched, good vigour
BLOCK III					
0-16-0	140	270	2350	47.8	Dwarfed, poor vigour.
0-16-8	100	180	4740	81.5	Foliage light green, vigour reduced.
0-16-16	72	180	3940	85.1	Foliage yellow green, reduced in vigour.
2-0-0	170	212	700	33.3	Severe scorch, poor vigour.
2-0-16	288	42	3420	88.9	Foliage normal, medium good growth.

Parts per million N	P	K	Yield	Growth notes
BLOCK II				
225	180	700	40.3	Reduced in vigour, dwarfed, foliage scorching.
82	170	6540	61.1	Foliage light green, vigour only fair.
62	180	6600	71.5	Foliage light green, reduced in vigour.
68	300	1600	28.1	Foliage light green, vigour poor.
30	170	2360	52.6	Foliage yellow green, weak growth.
45	240	1316	46.2	Poor vigour, foliage light green, severe scorch.
70	200	3430	85.6	Foliage slightly light green, medium vigour.
65	203	5900	54.0	Foliage yellow green, reduced in vigour.
450	243	640	34.1	Foliage dull green, severely scorched, vigour poor.
232	160	3950	90.8	Foliage normal, medium vigour.
195	210	8400	90.6	Foliage normal, medium to good vigour.
240	246	250	32.9	Dwarfed, severe scorching.
195	190	2630	93.2	Normal colour, medium vigour.
195	230	3640	104.1	
215	280	2160	43.0	Dwarfing, severe scorch.
110	183	4740	96.0	Foliage slightly light green, med. vigour.
190	260	3140	81.1	Foliage slightly light green, vigour med.
385	146	680	41.9	Dwarfed, severe scorch.
310	160	3140	89.7	Foliage normal, medium vigour.
203	60	3140	92.6	Foliage normal, vigour fair.
205	170	1830	34.5	Scorching, dull green, dwarfed.
179	160	3140	98.5	Foliage normal, good vigour.
330	241	500	64.0	Medium scorching, fair to poor vigour.
285	176	5000	100.9	Foliage medium green, good vigour.

Field observations showed definite potassium deficiency symptoms in the plant with levels of 2100 p.p.m. and below in the plant tissues.

Relationship between Levels of Phosphorus in the Plant Tissues and Yields

After the effects of nitrogen and potassium are accounted for there is a significant negative relationship between levels of phosphorus in the tissues and yields ($r = -.493$). There are only three instances where phosphorus levels drop below 100 p.p.m. and even with levels of 42 or 46 p.p.m. there is no apparent reduction in yield.

The relationship between phosphorus and yield changes with different values of potassium. In the range of potassium 250-3000, nitrogen and potassium effects accounted for there is a significant negative relationship between levels of phosphorus and yields ($r = -.631$), while with potassium above 4000 there is no relationship between phosphorus levels and yields ($r = +.047$).

Relationship between Levels of Nitrogen in the Plant Tissues and Yields

When the nitrogen levels are divided into two categories 30-200, and 200-1000 p.p.m. the following relationships appear. With a range of nitrogen up to 200 p.p.m. there is a positive relationship between nitrogen and yield ($r = +.343$) after phosphorus and potassium are accounted for. This result is different from that found in 1944, when no relationship was found within this range of nitrogen. With a range of nitrogen from 200-1000 there is a negative relationship between nitrogen and yield ($r = -.609$). However, as was the case in 1944, in the majority of cases of high nitrogen and low yields, phosphorus is also at a high level and potassium at a low level. With potassium accounted for there is a positive relationship between nitrogen and phosphorus ($r = +.443$). With phosphorus accounted for there is no relationship between nitrogen and potassium ($r = -.153$) and with nitrogen accounted for there is no relationship between phosphorus and potassium ($r = -.153$). There is, however, a significant negative relationship between the combined nitrogen and phosphorus unit on potassium levels ($R = .526$).

The effects of nitrogen or phosphorus levels on yield appear to be largely conditioned by the potassium content. It has already been pointed out that there is a significant negative relationship between phosphorus and yield only when the potassium level is not above 3000 p.p.m., and that there is a relationship between low potassium levels and combined high levels of phosphorus and nitrogen.

RESULTS, 1946

The parts per million of soluble nitrogen, phosphorus, potassium, calcium and magnesium found in the tissues along with fertilizer treatments and yields are shown in Table 3.

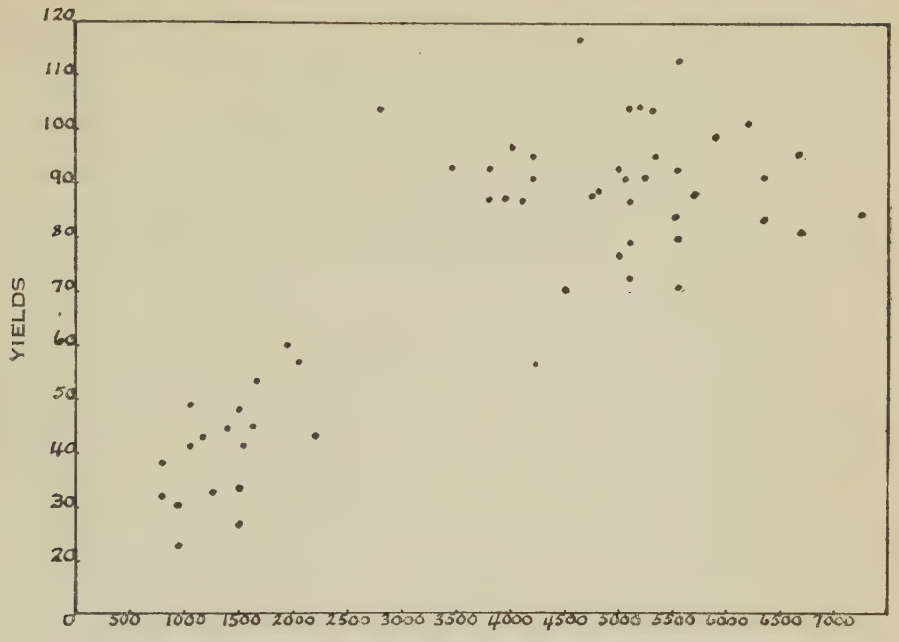
Relationship between Fertilizers Applied and Levels Found in the Plant Tissues

The application of potassium is generally reflected in increased potassium in the tissues. The average level of potassium in the tissues for all plots not receiving potassium is 1383 p.p.m. and the average yield 41;

TABLE 3

Fertilizer formula	Block I						Block II					
	Parts per million					Yield	Parts per million					Yield
	N	P	K	Mg	Ca		N	P	K	Mg	Ca	
0-0-0	82	169	2200	1300	500	43.5	56	93	2020	725	520	57.5
0-0-8	60	48	5100	367	40	73.0	54	74	4500	435	70	70.5
0-0-16	81	23	5550	430	70	80.0	115	49	4800	280	70	88.5
0-8-0	125	177	1950	1210	600	60.0	275	211	1500	1090	660	33.5
0-8-8	47	100	4200	290	490	56.5	94	88	4100	510	250	87.5
0-8-16	88	90	5750	240	660	88.0	94	67	5200	500	125	104.5
0-16-0	165	110	800	950	670	38.0	300	246	1500	1090	710	26.5
0-16-8	98	118	6350	433	200	83.5	125	89	5000	380	330	93.0
0-16-16	66	75	5550	360	450	92.5	100	56	3800	385	100	93.5
2-0-0	164	150	1250	1180	540	32.5	460	82	1050	1050	640	40.5
2-0-8	226	34	5550	565	200	71.5	181	30	4200	590	150	91.5
2-0-16	49	57	6200	400	40	101.5	244	17	3800	440	110	87.5
2-8-0	241	128	800	950	680	32.0	234	168	1150	1150	700	43.5
2-8-8	103	67	3450	440	200	93.5	127	75	5350	350	90	95.0
2-8-16	106	92	5100	375	100	79.5	100	52	5550	240	40	113.0
2-16-0	326	154	1650	1200	830	53.5	620	207	1550	1110	690	41.0
2-16-8	175	83	4750	290	140	88.5	125	76	4200	510	120	95.5
2-16-16	241	83	5100	380	110	87.0	156	107	5100	350	250	104.0
4-0-0	745	128	950	1150	760	30.0	639	69	1650	1150	660	44.5
4-0-8	214	100	5900	465	50	99.0	194	29	5550	535	140	84.0
4-0-16	280	17	5000	420	50	77.5	88	27	4000	300	110	97.5
4-8-0	229	181	1020	1110	790	49.0	694	145	950	925	860	22.0
4-8-8	67	89	2800	350	80	104.0	49	89	5100	325	110	91.0
4-8-16	85	73	3900	330	40	87.5	175	82	6700	130	120	81.5
4-16-0	556	222	1400	1050	830	44.5	535	165	1500	1050	790	48.0
4-16-8	47	85	4650	350	100	117.5	68	122	5350	350	240	104.5
4-16-16	214	53	6350	285	40	91.0	170	87	5250	415	110	91.5

DIAGRAM 3



for plots receiving 8 units in the formula or 120 pounds of K_2O per acre the average level is 4783 p.p.m. and the average yield 88.8 and for all plots receiving 16 units or 240 lb. of K_2O per acre the average level is 5150 p.p.m. and the average yield 91.4.

The application of phosphorus only is reflected in increased phosphorus in the tissue and a reduction of potassium but when applied along with potassium the phosphorus levels are not increased. The application of nitrogen is reflected in increased nitrogen in the tissues. The average level of nitrogen in the tissues for all plots not receiving nitrogen is 113 p.p.m. and the average yield 70.5; for plots receiving 2 units or 30 lb. of nitrogen per acre the average level is 215 p.p.m. and the average yield 75 and for all plots receiving 4 units or 60 lb. of nitrogen per acre the average level is 280 p.p.m. and the average yield 75.8.

Relationship between Levels of Potassium in the Plant Tissues and Yields

The relationship between levels of potassium in the plant tissues and yields is shown in Spot Diagram 3. When the effects of nitrogen and phosphorus are accounted for there is a positive relationship over the total range between potassium in the tissues and yields ($r = + .562$). With levels of potassium above 3000 there is no relationship with yield ($r = + .034$), while with levels below 3000 p.p.m. there is a high positive relationship ($r = + .752$).

Relationship between Levels of Phosphorus in the Plant Tissues and Yields

After the effects of nitrogen and potassium are accounted for there is a significant negative relationship between levels of phosphorus in the tissues and yields ($r = -.325$). From the lowest level of phosphorus up to 70 p.p.m. there is no relationship ($r = +.086$); with levels of phosphorus above 70 p.p.m. there is a negative relationship ($r = -.384$).

The relationship between phosphorus and yield in each of the two categories of potassium is not significant, although there is an apparent difference in trend. With potassium 800-3000 the correlation coefficient between phosphorus and yield is ($r = -.324$), while with potassium 3000 and up the coefficient is ($r = +.151$).

Relationship between Levels of Nitrogen in the Plant Tissues and Yields

Over the whole range there is a significant negative relationship between levels of nitrogen and yields ($r = -.354$), with phosphorus and potassium accounted for.

However, as was the case in the previous two years, in the majority of cases of high nitrogen and low yield phosphorus is also at a high level and potassium at a low level. With phosphorus accounted for there is a negative relationship between nitrogen and potassium ($r = -.428$) and there is a highly significant negative relationship between the combined nitrogen and phosphorus unit and potassium levels ($R = .773$). As in 1945 the effects of nitrogen and phosphorus levels on yield appear to be largely conditioned by the potassium content.

Relationship between Levels of Magnesium and Potassium

This relationship is shown by means of Spot Diagram 4. It will be observed that it is the exact counterpart of Diagram 3, illustrating the relationship between potassium levels and yields. There is a highly significant negative relationship over the whole range between levels of potassium and magnesium ($r = -.881$). Low potassium in the tissue is associated with an accumulation of magnesium.

Relationship between Levels of Calcium and Potassium

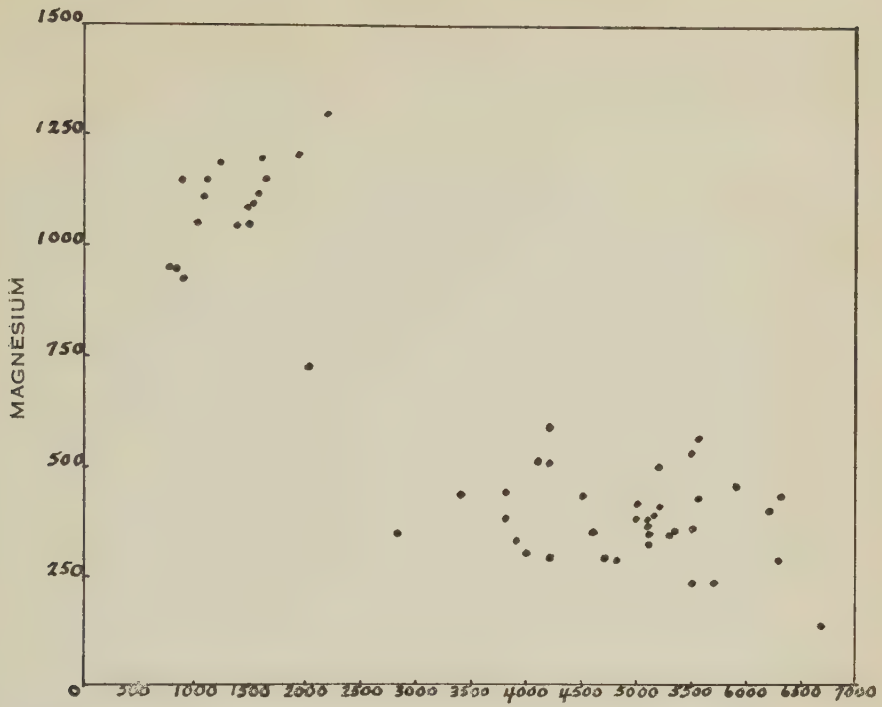
Over the whole range there is a significant negative relationship between levels of potassium and calcium ($r = -.826$). Low potassium in the tissue is associated with an accumulation of calcium.

DISCUSSION

The application of potassium as a fertilizer to this muck soil is reflected in increased levels of soluble potassium in the lower petioles of the potato plant by the methods of tissue analyses employed. Thus, over the whole range of treatments the application of 120 pounds of potash per acre increased the average level in the tissue by approximately 2900 p.p.m. and the application of 240 pounds per acre increased the average level in the tissue by approximately 3770 p.p.m.

The application of phosphorus only is reflected in increased phosphorus in the tissue and a reduction of the potassium level, but when applied along with either nitrogen or potassium interaction effects occur.

DIAGRAM 4



Potassium is the predominating fertilizer element affecting yield and analyses of the tissues in three successive seasons indicated that if plants contain less than 3500 to 4000 p.p.m. yield will be depressed. Field observations showed definite potassium deficiency symptoms in the plant with levels of 2100 p.p.m. and below in the plant tissues. Carolus (1) suggested a minimum K_2O content of 2200 at the beginning and 4500 p.p.m. at the end of the season. In studies conducted by Lorenz (8) soluble potash never ranged less than 10,000 p.p.m. (8301K) even on plots lacking potassium additions and in these studies the application of potassium did not increase yield.

Over the whole range there is a negative relationship between levels of phosphorus in the tissues and yield. There appears to be a change in this relationship between the lower and higher levels of phosphorus; from the lowest level of phosphorus up to 70 p.p.m. there is no relationship, while with levels of phosphorus above 70 p.p.m. there is a negative relationship. This relationship between the higher category of phosphorus and yield appears to hold only when the high phosphorus level is associated with low potassium (below 3000) in the tissue. If potassium in the tissue is above this figure there is no relationship between phosphorus and yield. Unless potassium is available in sufficient supply the application of phosphorus is likely to depress yield.

Carolus (1) found that a minimum soluble phosphorus content of 150 at the beginning and 60 at the close of the season was necessary for maintaining high yields. Lorenz (8), however, has presented data which showed

no significant decrease in yield with plants that had 52 p.p.m. of soluble phosphorus at the beginning of growth and 23 p.p.m. at the end of the season. In the present studies there was no apparent reduction in yield with phosphorus levels at 42 or 46 p.p.m.

Nicholas (10) has reported a case where chemical values of soluble phosphorus did not agree with the visual data and suggests that the tissue test method for determining phosphate in "acid" plants must be re-examined to establish whether the values accord with the total phosphorus content. With preliminary studies conducted in sand culture it was found that the soluble phosphorus in the plant need increase but very little between plants much reduced in vigour and showing symptoms of phosphorus deficiency, and plants that were quite vigorous and healthy in appearance. There was a much wider gradient in total phosphorus content. It is possible that the optimum level of soluble phosphorus is so critical as to be difficult to determine. Further studies are being conducted along this line.

Over the whole range there is a significant negative relationship between levels of nitrogen in the plant tissues and yields. When the nitrogen levels are divided into two categories there is no relationship (1944) or a positive relationship (1945) with levels up to 200 p.p.m. and field observations show that plants below this level had light green foliage indicative of nitrogen deficiency. With a range of nitrogen from 200-1000 there is a negative relationship between nitrogen and yield. However, in the majority of cases of high nitrogen and low yields, phosphorus is also at a high level and potassium at a low level. There is a significant negative relationship between the combined nitrogen and phosphorus unit on potassium levels.

In field experiments Cowie (3) has found that leaf scorch and other potassium deficiency symptoms on aerial parts of the plant are normally induced by nitrogen-phosphorus treatment and not by nitrogen treatment. An interaction between nitrogen and phosphorus is the primary factor inducing potassium symptoms in the aerial parts of the plant.

The effects of the higher nitrogen or phosphorus levels on yield in these studies are largely conditioned by the potassium content and it has already been pointed out that there is a significant negative relationship between phosphorus and yield only when the potassium level is below 3000 p.p.m.

Carolus (1) has suggested a minimum soluble nitrogen content of 700-800 p.p.m. and Lorenz (8) has also suggested that if plants contain less than 800 p.p.m. of nitrate approximately one month after emergence the yield will be depressed. In these studies levels of over 200 p.p.m. did not appear to increase yield.

There is a highly significant negative relationship between levels of potassium and magnesium in the plant tissue. Low potassium in the tissue is associated with an accumulation of magnesium.

The average magnesium content for all plots with yields above 90 is 365 p.p.m. and it would appear that a magnesium content of approximately this level is adequate to promote optimum yield.

Carolus (1) suggested a minimum magnesia content of 275 (165 mg.) at the beginning and 800 p.p.m. (480 mg.) at the end of the season.

There is also a negative relationship between levels of potassium and calcium in the plant tissue. Low potassium in the tissue is associated with an accumulation of calcium.

SUMMARY

A study was made of critical nutrient levels with yields in the conducting tissue of potato at one stage of growth. Samples were taken from field plots on a muck soil, involving the application of three levels of nitrogen, phosphoric acid and potash arranged as a factorial experiment.

The application of fertilizers is reflected in the lower petioles of the plant by the methods of tissue analyses employed. Tissue analyses indicated that if plants contain less than 3500 to 4000 p.p.m. of potassium, yield will be depressed. From the lowest level of phosphorus up to 70 p.p.m. there is no relationship with yield but with levels above 70 p.p.m. there is a negative relationship. This negative relationship only holds if the potassium level is below 3000 p.p.m.

With nitrogen up to 200 p.p.m. there is probably a positive relationship with yield, while with nitrogen from 200-1000 there is a negative relationship with yield.

There is a significant negative relationship between the combined nitrogen and phosphorus unit on potassium levels and the effects of the higher categories of nitrogen or phosphorus levels on yield are largely conditioned by the potassium level.

A negative relationship exists between levels of potassium and magnesium and between potassium and calcium. Low potassium in the tissue is associated with an accumulation of magnesium and calcium.

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DITYLENCHUS RADICICOLA (GREEFF) FILIPJEV, A ROOT-GALL NEMATODE NEW TO CANADA, FOUND ON WHEAT AND OTHER GRAMINEAE[1]

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In February, 1947, a few plants of Thatcher wheat with numerous galls on their roots were received from a farmer north of Radisson, Saskatchewan. These plants were about seven weeks old and had been grown indoors in a shallow box of soil which came from a 15-acre field in a low-lying meadow or "slough bottom" (Figure 1). The field of virgin sod was ploughed up during the previous summer and had been dry for several years following the prolonged droughts of the 'thirties; formerly it was more or less steadily under water. The soil in which the plants were grown was collected late in the autumn and sown to two rows each of spring wheat (var. Thatcher), winter wheat (var. Kharkov), rye (var. Prolific) and oats (var. Banner) in a flat near the kitchen window. The farmer had found galls on the roots of the spring and winter wheats, but not on the rye and oats. On the roots of a single wheat plant he counted 44 galls. He had concluded from his own experiment that it would be safe to grow either rye or oats on his infested 15-acre field.

[1] Contribution from the Laboratory of Plant Pathology, University of Saskatchewan, Saskatoon, Sask., with financial assistance from the Saskatchewan Agricultural Research Foundation.

[2] Professor of Plant Pathology.

FIGURE 1. General view of the nematode-infested field and surrounding country at Radisson, June 16, 1947. Oats at *left*, wheat at *centre*, virgin prairie at *right* and *middle distance* (light strip), and wheat *in distance*.

EXAMINATION OF THE ROOT GALLS

The majority of galls are produced on branch roots either along their course or, less frequently, at their tips (Figures 2 and 3). Mature galls are 2-6 mm. long by 2-4 mm. wide. They are normally curved with a slight twisting tendency in a semi-circular arch which tapers more gradually towards its lower end. The galls are ordinarily free of root hairs. The portion of the root below the gall is consistently thicker than that above the gall (Figures 4, 5, *e* and 6). Old galls about to disintegrate are light brown to brown in colour, with usually a dark brown area on the inner side of the arch (Figures 4, *n* and 5, *n*). By clearing the galls in lactophenol and by free-hand sectioning, it can be seen that both the central vascular cylinder and the cortex are enlarged. The nematodes and eggs appear to be confined to the cortex.

On dissecting mature root galls in a drop of water under a dissecting microscope, a few nematodes and abundant eggs could be observed issuing from the galls. Under the compound microscope the adult worms could be distinguished as male and female; the majority of eggs were seen to be embryonated, and newly hatched larvae were commonly found.

In general appearance these galls do not resemble those reported by Russell (6) and Thorne (8) on the roots of wheat in Saskatchewan caused by the wheat nematode, *Heterodera punctata* Thorne, and are not likely to be confused with them. Furthermore, *D. radicicola* does not form nematode cysts while *H. punctata* does.

THE ORGANISM

The bodies of adults of both sexes were widest in the middle, tapering towards both extremities, the tail being very sharply pointed. The female was strongly and the male slightly curved. The females averaged 1.77 mm. in length by 0.06-0.07 mm. in width, and the males 1.43 mm. by 0.05 mm. The eggs were cylindrical with rounded ends and measured 86 μ by 37-38 μ.

All the finer morphological details fitted most closely the description given by Goodey (4) for *Anguillulina radicicola* (Greeff) Goodey, which is now a synonym of *Ditylenchus radicicola* (Greeff) Filipjev (2). However, the measurements for the Saskatchewan strain are near the lower limits of those given by Goodey. Studies on host range, as reported later, tended to confirm this diagnosis. There is the possibility that further detailed studies might prove our form to possess some features not shared by the European forms. Goodey found that eight to nine weeks elapse between infection of the roots by young larvae and the escape of larvae of the next generation from their egg-cases. It seems that the complete life-cycle of the Saskatchewan strain is in agreement with this.

HISTORY

A full historical account of reports on this nematode are given by Goodey (4). It was first found by Greeff on annual meadow-grass and couch grass in Germany in 1864. Since that date it has been reported on the roots of grasses and cereals in Sweden, Norway, Denmark, Finland, Scotland and England. Goodey points out that its geographic range

extends from within the Arctic circle to the vicinity of Bonn, Germany. Radisson is well within this range of latitude. The nematode has not hitherto been reported outside northern Europe.

There is a report by Ledingham (5) in 1937, which might possibly refer to the same organism in Saskatchewan. He found nodules or galls on the seminal roots of wheat seedlings collected near Fish Creek on June 4, 1937. The galls were likened to those found on legumes and appeared to contain a mass of bacteria, but he concluded that further observations on this point were necessary. R. J. Ledingham has informed me that gall formation was readily obtained on the roots of wheat grown in Fish Creek soil in the greenhouse in 1937. Baker (1) apparently assumes that the nodules on wheat roots reported from near Rosthern, Saskatchewan, in 1937 (7) were possibly caused by nematodes. Both this (7) and the Fish Creek report of Ledingham (5) refer to the same outbreak.

EXPERIMENTAL STUDIES

Greenhouse Studies with Radisson Soil

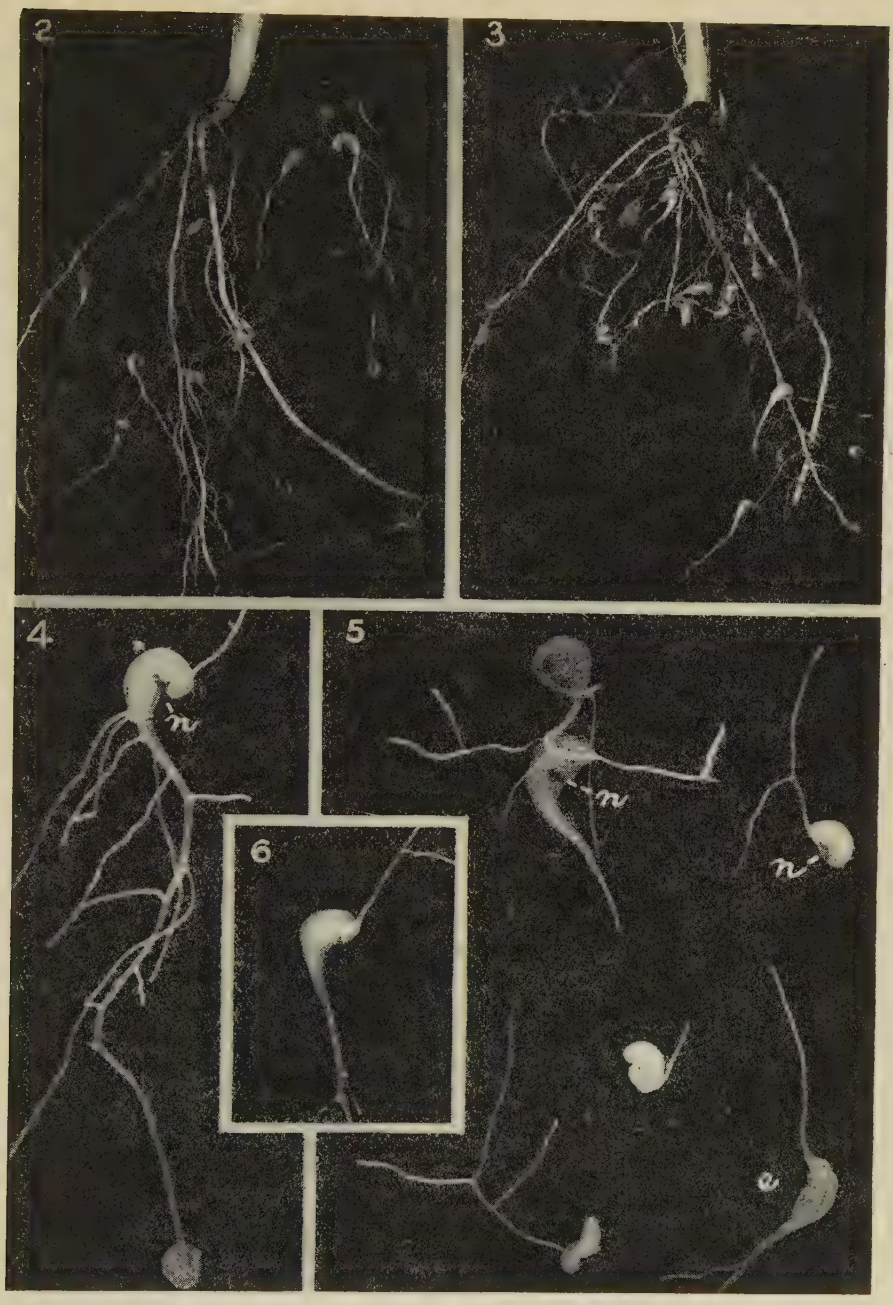
About 75 pounds of soil were obtained from the nematode-infested field in March, 1947. It is a peaty loam, very uneven in texture with abundant undecomposed plant roots and slatey-coloured, cloddy lumps intermixed. Its reaction varied between pH 7.5 and 7.8 in different tests. Effervescence was strong, sulphates low and chlorides absent.

This soil, after thorough mixing and removal of large fibrous clods, was potted out and sown to various crops in the greenhouse. The roots of the plants were examined for galls after seven, eight and nine weeks with the following results: Infestation was moderate to heavy on wheat (var. Thatcher), moderate on barley (var. Plush) and *Agropyron cristatum* (L.) Gaertn., and light on rye (var. Prolific); no galls were found on oats (var. Exeter), maize, *Bromus inermis* Leyss., flax (var. Royal), Argentine rape, sunflower (var. Mennonite), alfalfa (var. Grimm) and sweet clover (var. Redfield Yellow). *A. cristatum* has not previously been infected.

This experiment was repeated on the gramineous hosts in July and August, again under greenhouse conditions. Only traces of gall formation were found on wheat and none on the other crops. The extremely high summer temperatures, especially from July 7 to 15, when the maximum daily temperature was over 90° F., may have accounted for the decrease in infestation. In a third experiment, cereals were grown in a mixture of soil from the earlier experiments and some fresh soil collected in July. These were sown on September 16 and the roots examined on November 12. Again traces of gall formation were found on wheat only.

Greenhouse Studies with Fish Creek Soil

In view of the finding of the root-gall nematode in wheat roots from Radisson and of the undetermined nature of the cause of the galls on wheat roots from Fish Creek in 1937, several attempts were made to obtain galls on wheat by growing wheat in soil from the Fish Creek field collected in the early spring of 1947. In no instance was gall formation secured.



FIGURES 2 to 6. Galls on wheat caused by *D. radicicola*.

FIGURES 2 and 3. Slightly less than natural size.

FIGURES 4, 5, and 6. The larger diameter of the roots below the galls is seen in Figures 4, 5, *e* and 6, and the darker necrotic areas at *n* in Figures 4 and 5. (Magn. × 2.5).

Field Studies

On May 8, the infested field at Radisson was sown to oats with the exception of one drill-width at one side which was sown to Thatcher wheat. This field was visited on June 16. A very light gall infestation was found on the wheat roots and none on the oat roots. At this time blocks of virgin sod were dug up at distances up to about one rod from the edge of the field under crop, and brought into the laboratory for careful examination. A few galls were found on one species of grass only, which, when potted and allowed to flower, proved to be *Agropyron smithii* Rydb. (western couch-grass), a native form. It seems, therefore, that *Ditylenchus radicicola* is indigenous to northern Saskatchewan. Natural infections on wheat and *A. smithii* have not previously been reported (cf. 3 and 4).

The field was again visited on July 21. Except for a patch of about two acres in a low spot in the oat field, both crops were dying from drought and strong competition from weeds, mainly Russian thistle (*Salsola pestifer* A. Nels). The crops were complete failures as the field was disked shortly afterwards to prevent the weeds from going to seed. The rainfall for the district was 0.52 inches in May, 0.99 inches in June and 0.53 inches in July. This was far too meagre for the newly ploughed peaty soil to support a crop. No galls were found on the wheat roots examined at this date.

Wheat growing in a field which had been under cultivation for several years and situated about half a mile from the infested field was examined for galls (Figure 1). None was found on its roots.

DISCUSSION

The root-gall nematode appears to be indigenous on native grasses in northern Saskatchewan and has been found capable of attacking wheat under field conditions. Since gall formation on the roots of both spring and winter wheat may be quite conspicuous, the question arises as to why infestations have not been found before; that is, with the possible exception of the Fish Creek report in 1937 as previously mentioned. The high resistance of oats (cf. 4), the immunity of dicotyledonous hosts and the practice of summer-fallowing, are doubtless among the factors responsible for starving out the parasite, or keeping its population to such a low degree that its presence has hitherto passed unnoticed. Further, it is probable that the nematode is favoured by cool, wet conditions such as are found in "slough bottoms". With the gradual drying up and subsequent cultivation of such areas, conditions unfavourable to the parasite are produced. If the first crops on "slough-bottom" land do not thrive, growers would be inclined to attribute the cause to abnormal soil conditions, such as alkalinity, poor texture, mineral deficiencies or imbalance. Assuming, therefore, that the first crop of wheat on the new land was infested with the nematode, by the time wheat was grown again, infestation might be considerably reduced or possibly eliminated. Also, if the Fish Creek infestion was caused by nematodes, then it seems that the crop practices on the prairies are well suited to the reduction and subsequent possible eradication of the parasite. This is borne out by the absence of galls on wheat roots in the old field near to the infested one at Radisson. A similar case in point is the apparent disappearance of the wheat nematode, *H. punctata*, which has not been found in recent years in fields in which it was formerly common.

The discovery in Saskatchewan of the root-gall nematode which is found capable of attacking wheat in the field and of causing appreciable damage on wheat under experimental conditions is of considerable interest. Because of the known resistance of this nematode to desiccation (4), there is the chance that quiescent larvae may remain in that state for a long time, only to survive when conditions become more favourable. During the next few years, therefore, the Radisson field should be kept under observation as a necessary precaution. The evidence outlined above, however, suggests that a proper crop rotation and periodical summer-fallowing should go a long way to remove the menace.

SUMMARY

The root-gall nematode *Ditylenchus radicicola* (Greeff) Filipjev was found in 1947 attacking wheat and *Agropyron smithii* Rydb., a native grass, in northern Saskatchewan and is, therefore, probably indigenous. The field was a low meadow ploughed for the first time during the previous summer. The present report is the first outside northern Europe. It is also the first report of natural infection on wheat and *A. smithii.*

Experimental infection was secured on barley (var. Plush), rye (var. Prolific), and *Agropyron cristatum* (L.) Gaertn.; no galls developed on oats (var. Exeter), maize, *Bromus inermis* Leyss., flax (var. Royal), Argentine rape, sunflower (var. Mennonite), alfalfa (var. Grimm) and sweet clover (var. Redfield Yellow). *A. cristatum* has not previously been infected.

Though this nematode is capable of causing appreciable gall formation on wheat roots, it is considered that adequate control should be secured in due course by combining a suitable crop rotation with summerfallowing; nevertheless, it is suggested that the infested area be kept under observation during the next few years as a necessary precaution.

ACKNOWLEDGMENTS

The kindly co-operation of Wasyl Petriew, Radisson, on whose farm the infestation occurred, is greatly appreciated. The author is also much indebted to A. D. Baker, Division of Entomology, Department of Agriculture, Ottawa, for confirming the diagnosis and critically reading the manuscript.

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PERMEABLE SEEDED STRAINS OF SWEET CLOVER (*MELILOTUS ALBA*), THEIR DEVELOPMENT AND NATURE[1]

W. J. White and T. M. Stevenson

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It is a generally well known fact that when harvested without any abrasive action a very low proportion of sweet clover seed is permeable to moisture. Stevenson (8) collected mature open-pollinated seed from 10,982 single plants of *M. alba* in the fall of 1931 and found that as an average only 0.66 per cent of the seed was permeable. He found that the seed from 98.75 per cent of the plant population displayed a permeability ranging between 0 and 4 per cent and that the balance of the population ranged between 5 and 8 per cent permeability. Martin (7) made collections of sweet clover seed in the late summer and early fall each year for 10 years and using hand hulled mature seed found that the germination in November averaged 9 per cent. Martin states that "despite the softening effects of the abrasions and other injuries of seed coats by combines or whatever type of harvester used, hardness still ranges as a rule from 60 to 80 per cent."

The hardness or impermeability has been shown by Coe and Martin (1) to be caused by the structure of the seed coat. To overcome the impermeable condition seed intended for sowing is generally scarified. This process simply cracks, chips, or scratches the seed coat sufficiently to allow moisture to permeate the seed.

The work of Martin (7) has demonstrated that hard seed will soften to the extent of 80 to 100 per cent when stored from October to April in an open unheated building. Fluctuating temperatures in the realm of freezing for a period of two or more months was apparently the factor largely responsible for softening the seed coats. When hard seeds were stored from October to April in soil under field conditions at depths of 1, 3, 6, 9, and 30 inches, Martin found that "the softening varied somewhat inversely with the depth, to the depth of 9 inches." The hardness of the seed at the 30-inch depth was not altered apparently due to the fact that in Iowa the soil seldom freezes to that depth. Even at the 3-inch depth, however, from 32 to 50 per cent of seed was still hard in the spring.

These studies by Martin provide an explanation for the fact that when unscarified or improperly scarified sweet clover seed is sown the crop may volunteer for many years. Stoa (10) presents the history of one field on which seed shattered naturally prior to harvest and mechanically during the harvesting operations in the fall of 1917. In the fourteen-year period from 1918 to 1932 inclusive there were eleven distinct and generally heavy volunteer crops of sweet clover on this field traceable to the seed shattered in 1917. Stoa considered that "delayed tillage in some years, allowing more complete emergence, and more careful observation would in all probability have made possible recording volunteer growth in each of the fourteen years since 1918". Sampling areas 6 × 8 inches to a depth of 6 inches revealed that in 1931 there was still an average of forty hard but viable seeds per sample volume of soil.

[1] Contribution from the Division of Forage Plants, Experimental Farms Service, Dominion Department of Agriculture, Ottawa, Canada.
[2] Officer-in-Charge, Dominion Forage Crops Laboratory, Saskatoon, Sask.
[3] Dominion Agrostologist, Central Experimental Farm, Ottawa, Ont.

Recognizing that the development of a naturally permeable seeded variety would very materially aid in overcoming the problem of volunteering so commonly experienced in impermeable seeded varieties, Stevenson (8) began a selection program designed to develop permeable seeded strains. He found the permeability of the seed of 360 plants from the Arctic variety to range between 0 to 100 per cent and he used the open-pollinated seed from twenty-five plants which had a permeability of 10 per cent or higher to establish lines. Selection was continued in these lines through two generations of inbreeding. Due to abnormalities appearing upon inbreeding he was only able to work with five lines. He showed that for these five lines the average permeability at the end of the second inbred generation ranged between 16.47 per cent and 33.36 per cent whereas the open-pollinated progenies from the originally selected plants ranged between 0.82 per cent and 5.85 per cent permeability. Thus he demonstrated that considerable improvement in permeability had been attained through selection in lines inbred for two generations.

This paper reports upon the progress to date of the selection program initiated by Stevenson and upon the result of hybridization of permeable seeded lines with other permeable seed lines and with non-permeable seeded lines. It also presents data relative to the nature of the permeability. In the course of this study from 1933 to 1945 permeability tests have been conducted on approximately 23,000 plants.

MATERIALS AND METHODS

Of the twenty-five plants selected in 1931 which had from 10 to 100 per cent permeable seed, only five gave rise to strains which were normal enough in vegetative and reproductive characters after one to two generations of inbreeding to permit their being carried along. Due to superior permeability only two of these original five strains were continued after 1937. The original selection numbers of these two strains were S-30-11 and S-28-5b. The S-30-11 strain was discarded in 1943 because it carried a gene or genes for a semi-dwarf habit of growth.

A loss of vigor accompanied continuous selection in inbred lines. In an effort to recover vigor crosses were made in the field in 1939 between the two lines then being worked with and between one of these lines and the Pioneer variety (9). In the 1944-45 nursery these crosses had been advanced to the F_4.

Throughout the duration of the project, mature open-pollinated seed has been collected from each plant in the single plant nurseries by hand stripping the seed from the racemes. Until 1945 the dehulling was done by rubbing the seed between the palms of the hands. In 1945 a corrugated rubber mat and rubber covered block were used. A sample of 50 well developed seeds from each plant was counted out and placed in a small glass vial. A few drops of water were added to each vial. The vials were then loosely stoppered and placed in an inclined position in a tray. Until 1937 permeability readings were taken on the seventh and repeated on the fourteenth day after the test was commenced. The records showed that there was practically no change in permeability from the seventh to fourteenth day. Thus commencing with the 1939 testing and continuing

since then permeability counts have been made on the fifth day. The duration of the permeability test thus conforms to the duration of the official germination test employed by the Production Service, Plant Products Division (11) in testing sweet clover for germination in Canada.

In determining permeability all seeds which had swollen whether they had germinated or not were counted as permeable. A high proportion of the seeds was generally immersed in the water in the vial. This condition prevented or restricted germination. By running duplicate tests of some plants on sand in Petri dishes it was found that the percentage permeability in water in vials corresponded almost exactly with the germination on sand. The vial test thus gave the information desired and was more convenient than Petri dish tests.

The reliability of the vial test was further checked by having germination tests conducted on a random group of plants by the seed testing

TABLE 1.—RELATIONSHIP BETWEEN PERMEABILITY OF UNSCARIFIED SEEDS OF SINGLE PLANTS WHEN DETERMINED BY GLASS VIAL TEST AND BY OFFICIAL GERMINATION TEST METHODS OF PRODUCTION SERVICE, PLANT PRODUCTS, SASKATOON

Strain No.	Percentage of permeable seeds as determined by		Official germination, %**
	Official test*	Vial test	
Study No. 1—Official germination on 100 seeds; vial test on 50 seeds.			
407-42-5	88	96	96
407-42-10	96	98	99
407-42-13	97	96	100
407-42-15	99	98	98
407-42-20	96	100	99
407-42-24	91	92	98
407-43-25	96	98	100
407-43-38	95	98	100
407-44-9	4	0	99
407-46-9	94	90	95
407-46-18	100	94	96
407-46-29	1	0	100
Average	79.75	80.00	98.33
Study No. 2—Official germination and vial test on 50 seeds.			
S-42-16-2	100	100	100
S-42-16-1	92	100	90
S-42-13-4	92	88	88
S-42-13-2	98	96	96
S-42- 9-2	92	96	90
S-42- 9-1	94	94	92
S-42-18-1	94	100	92
Average	94.57	96.29	92.00

* Hard seed content subtracted from 100.
** Healthy seedling + hard seeds.

laboratory of the Production Service, Plant Products Division, Saskatoon. Table 1 presents the data from the official germination tests and from the vial tests on the same plants.

It is obvious from Table 1 that the permeability as determined by the vial test corresponds very closely with that determined by official germination testing methods. Such minor differences as are shown by the data are undoubtedly due to sampling differences. Furthermore there is a close correspondence between the percentage permeability and the official germination test in the case of permeable seeded plants. Determination of permeability by the vial test thus also gave a good measure of viability of the freshly harvested seed. It has been observed, however, that seed of permeable seeded plants discolours much more quickly as it ages than does hard seed of common varieties. Thus it is likely that with seed a few years old the vial test for permeability would not give a reliable index of viability.

Throughout the project selection has been made of plants having the highest attained permeability in lines or strains having the highest average permeability.

EXPERIMENTAL RESULTS AND DISCUSSION

Development of Highly Permeable Seeded Lines

A large proportion of the lines presently carried in the breeding nursery trace back to the single plant selection designated S-28-5b. The distributions of permeability of the seed of two open-pollinated generations and the following five selfed generations of this strain are given in Table 2.

From Table 2 it is seen that in the first open-pollinated progeny the modal class was the 2 to 9 per cent permeability class with the distribution ranging between the 0 and the 60 to 69 per cent class and mainly confined to the range 0 to 30 to 39 per cent classes. In contrast the S_5 ranged between the 60 to 69 and 98 to 100 per cent classes with the bulk of the population distributed between the 82 to 84 and 98 to 100 per cent classes. Disregarding the S_1 generation there is a progressive trend in each succeeding generation to a higher value for the modal class, and a narrowing of the range of distribution. This later trend is largely the result of the lower limits of distribution being confined to progressively higher class values. There appears also to be a trend from a multi- or bi-modal distribution to a uni-modal distribution, indicating the attainment of a higher degree of homozygosity in later generations. Aside from the rather high modal class value the characteristics of distribution of the S_1 generation comply with the trends described above.

A second strain which has been carried through six generations of selection traces back to a plant designated S-30-11. In Table 3 the distribution of permeability of the various generations of this line is given.

The improvement effected in the S-30-11 strain is less pronounced and more erratic than in the S-28-5b strain as is obvious from a study and comparison of Tables 2 and 3. It is seen, however, from Table 3 that there has been a more or less progressive decrease in the proportion of the population falling in the lower permeability classes. From the open-pollinated generation to the S_1 and the S_1 to S_4 and S_4 to S_5 there is a progression of higher modal class values. In the S_2 the bulk of the population was distributed in classes of moderately high permeability and that of the

TABLE 2.—FREQUENCY DISTRIBUTION OF PERMEABILITY VALUES OF POPULATIONS OF THE FIRST TWO OPEN-POLLINATED AND THE SUCCEEDING FIVE GENERATIONS OF SELFED PROGENIES DERIVED FROM PLANT S-28-5b

Generation	Year tested	Per cent of population in % permeability class														No. of plants tested
		0	2-9	10-19	20-29	30-39	40-49	50-59	60-69	70-76	78-80	82-84	86-88	90-92	94-96	98-100	
O.P.	1932-33	23.31	30.08	19.55	15.79	4.51	4.51	0.75	1.50	—	—	—	—	—	—	—	133
O.P.	1934-35	16.67	5.56	16.67	11.11	8.33	13.89	11.11	13.89	2.78	—	—	—	—	—	—	36
S_1	1936-37	—	—	—	7.70	3.08	12.31	6.15	9.23	18.46	20.00	10.77	1.54	1.54	7.70	1.54	65
S_2	1938-39	—	—	—	—	1.69	8.47	10.17	29.66	18.64	13.56	6.78	9.32	1.69	—	—	118
S_3	1940-41	—	—	—	—	—	—	5.81	12.79	27.91	11.63	12.79	12.79	6.98	8.14	1.16	86
S_4	1942-43	—	—	—	—	—	—	4.0	10.67	16.0	18.67	16.0	9.33	13.33	6.67	5.33	75
S_5	1944-45	—	—	—	—	—	—	—	1.00	3.01	4.76	9.02	16.79	28.07	28.57	8.77	399

TABLE 3.—FREQUENCY DISTRIBUTION OF PERMEABILITY VALUES OF POPULATIONS OF THE FIRST OPEN-POLLINATED AND THE SUCCEEDING FIVE GENERATIONS OF SELFED PROGENIES DERIVED FROM PLANT S-30-11

Generation	Year tested	Per cent of population in % permeability class														No. of plants tested
		0	2-0	10-19	20-29	30-39	40-49	50-59	60-69	70-76	78-80	82-84	86-88	90-92	94-96	98-100	
O.P.	1932-33	5.00	5.00	23.75	22.50	13.75	15.00	11.25	1.25	2.50	—	—	—	—	—	—	80
S_1	1934-35	3.03	3.03	3.03	15.15	18.18	24.24	18.18	9.09	—	3.03	3.03	—	—	—	—	33
S_2	1936-37	0.33	0.99	1.64	0.99	1.97	5.26	4.28	13.49	28.62	24.01	9.54	4.61	3.95	0.33	—	304
S_3	1938-39	—	2.67	9.50	21.86	16.22	25.81	13.16	9.40	0.89	0.49	—	—	—	—	—	1011
S_4	1940-41	0.27	0.53	0.27	1.60	4.01	9.09	8.29	19.52	18.18	13.64	8.29	9.36	6.15	0.80	—	374
S_5	1942-43	0.71	—	—	—	—	—	3.55	15.60	25.53	24.11	6.30	4.96	12.77	4.96	1.42	141

S_3 in exceptionally low permeability classes in comparison with the other generations. Aside from the possibility of seasonal climatic factors influencing permeability no plausible explanation can be offered for this variation between generations in distribution of permeability. However, even in the face of the noted variability it is obvious that considerable progress has been made in selecting for higher permeability in this strain. The distribution of permeability in the S_5 while fairly wide is in the moderately high classes. The bi-modal nature of the distribution in the S_5 suggests that considerable heterzygosity still exists.

Several lines have advanced into the F_4 generation from crosses involving S-30-11 with the Pioneer variety. The distribution of the permeability of the seed of F_2 plants and of plants of the F_3 and F_4 generations of two strains derived from this F_2 are given in Table 4.

TABLE 4.—FREQUENCY DISTRIBUTION OF F_2 OF S-30-11 × PIONEER AND OF THE F_3 AND F_4 OF TWO STRAINS DERIVED FROM THE F_2

Generation and strain	Per cent of population in % permeability class										Total no. of plants tested
	0	2-10	11-20	21-76	78-80	82-84	86-88	90-92	94-96	98-100	
F_4 of S-42-34	—	—	—	—	2.32	—	—	—	34.88	62.79	43
F_3 of S-42-34	—	—	—	6.06	3.03	—	—	39.39	45.45	6.67	33
F_2	13.16	50.00	5.26	10.52	—	2.63	—	5.26	5.26	7.89	38
F_3 of S-42-16	—	—	—	5.26	—	—	10.52	10.52	21.05	52.63	19
F_4 of S-42-16	—	—	—	0.91	1.82	6.36	3.64	10.91	69.09	7.27	110

It is seen from Table 4 that the permeability of the seed of the F_2 plants was distributed between the classes 0 to 98 to 100 with roughly 70 per cent of the population falling within the range 0 to 20 per cent and around 20 per cent within the range 90 to 100 per cent. By selection of the most highly permeable plants in the F_2 it is seen that the two F_3 progenies were comprised very largely of plants having seed which was highly permeable. In the one F_3 progeny 91.51 per cent and in the other 94.74 per cent of the population fell in the range of from 86 to 88 to 98 to 100 per cent permeability. In the case of strain S-42-34 the F_4 generation represented a considerable improvement over the F_3 but in the case of strain S-42-16 there is little or no evidence of such improvement from F_3 to F_4.

The data demonstrate that high permeability is inherited and the character can be recovered fairly readily from crosses with non-permeable material. It would appear quite feasible to develop lines combining high permeability with other desirable characters. In fact the S-42-16 line listed in Table 4 combines the type of low coumarin content of Pioneer with high seed coat permeability. It is of interest to note here that data presented in Table 5 show some of the lines derived from crosses to be somewhat superior in respect to permeability to the best lines derived by continuous selection.

A comparison of the permeability of the unscarified seed of the selected lines with that of unscarified seed of common varieties and with scarified seed being used by farmers is of interest. Information on the permeability

of commercial lots of seed was secured through the courtesy of the Saskatoon office of the Production Service, Plant Products Division, who made available their records covering 114 lots of sweet clover seed which had been submitted for germination tests. These records gave the hard seed content of each sample and for purposes of comparison the hard seed values were transposed to permeability values for each sample. Unfortunately in tabulating the data in these samples the class values of the frequency distribution table were somewhat different from those used in recording the data for the breeding stock. Consequently the comparison between these commercial samples and the best selected lines cannot be made in as great detail as might otherwise be the case. Nevertheless the data are of interest and are presented in Table 5 which also includes information on the permeability of unscarified seed of two varieties.

As seen from Table 5 the average permeability of the presumably scarified 114 commercial samples was 88.8 per cent. With one exception the permeability of unscarified seed of the selected lines exceeded that of the commercial samples. The permeability of the best line was approximately 10 per cent higher than the average of the commercial samples. The one exception noted above was the least permeable line of the S-28-5b strain tested and data pertaining to it were included in Table 5 merely to show the lower limit of permeability of lines of the S-28-5b strain. It is of interest to note that the average permeability of this line was just one per cent less than that of the commercial samples.

A large but undetermined proportion of the 114 commercial samples recorded in Table 5 had been submitted by seed companies for germination test. It is likely that the seed in most cases had been scarified with especially designed scarifiers. It seems very likely that farmers who grow their own seed and often scarify it with improvised equipment in most cases would not attain as high a degree of permeability as is indicated by the data presented for commercial samples in Table 5. It therefore seems justifiable to conclude that in respect to permeability the unscarified seed of the best selected lines is at least the equal to and likely is considerably superior to a large proportion of the scarified seed used by farmer growers.

Comparison of the permeability of the selected strains with that of unscarified Arctic and Pioneer requires no comment.

In respect to overcoming the problem of sweet clover volunteering in cultivated fields, it is obvious that the best naturally permeable seeded lines would be vastly superior to any of the varieties now used. Where sown these permeable seeded strains would germinate as well as the best scarified seed of common varieties and undoubtedly would germinate much better than much seed that is sown. Seed which shattered from plants of the naturally permeable seeded strains would germinate readily whereas shattered seed from common varieties is almost completely impermeable at the time of shattering and would only become permeable over a long period of time.

TABLE 5.—FREQUENCY DISTRIBUTION FOR PERCENTAGE PERMEABILITY OF THE MOST PERMEABLE SEEDED LINES IN THE 1945 NURSERY COMPARED TO UNSCARIFIED CHECK VARIETIES AND TO PRESUMABLY SCARIFIED COMMERCIAL LOTS OF SEED

Strain No. of variety	No. of plants with % permeability of										Ave. % perm.	No. of plants tested
	0	2-10	11-20	21-76	78-80	82-84	86-88	90-92	94-96	98-100		
	F_4 derivatives of crosses											
S-42-$\overline{34}$-1	—	—	—	—	—	—	—	—	7	22	98.2	29
S-42-36-1	—	—	—	—	—	—	—	5	25	8	95.4	38
S-42-$\overline{33}$-1	—	—	—	—	—	1	—	9	18	9	95.0	37
S-42-$\overline{18}$-2	—	—	—	—	—	—	3	2	25	3	94.5	33
S-42-$\overline{16}$-2	—	—	—	—	1	—	—	2	33	2	94.5	38
	Derivatives of continuous selection											
S-28-5b-$\overline{1}$-$\overline{5}$ (a)	—	—	—	—	1	—	4	11	13	11	93.8	40
S-28-5b-$\overline{1}$-$\overline{5}$ (b)	—	—	—	—	1	1	4	10	17	6	93.1	39
S-28-5b-$\overline{1}$-$\overline{5}$ (d)	—	—	—	—	—	2	5	6	15	5	93.0	33
S-28-5b-$\overline{1}$-$\overline{5}$ (c)	—	—	—	3	2	5	8	10	8	1	87.8	37
	Presumably scarified commercial samples*											
Commercial	—	—	2	19		8		85			88.8	** 114
	Unscarified Arctic and Pioneer											
Checks	35	57	5	1	—	—	—	—	—	—	3.6	98

* Distribution by samples not plants.
** Total number of samples not plants.

Permeability and Emergence in Soil under Field and Greenhouse Conditions

In the previous section all permeability data presented were obtained from the vial test. Studies were therefore set up to determine the permeability and emergence of various strains when the seed was sown in soil in both the greenhouse and field and the results obtained were compared to those secured from the vial test.

Seed of seven plants which had previously been tested by the vial technique were chosen for testing in unsterilized soil in flats in the greenhouse. One hundred open-pollinated seeds of each plant were sown in April, 1943 and the data obtained are presented in Table 6.

TABLE 6.—RELATIONSHIP BETWEEN PERMEABILITY OF UNSCARIFIED SEED OF HIGHLY PERMEABLE PLANTS IN WATER IN GLASS VIALS AND GERMINATION IN UNSTERILIZED SOIL IN THE GREENHOUSE

Strain No.	% Permeable seeds as determined on 50 seeds in vial test	% Germination in soil in greenhouse when seed was	
		Dusted with Ceresan	Not dusted
S-42-16-2	100	97	78
S-42-16-1	100	88	67
S-42-18-2	100	85	75
S-42-13-2	96	94	80
S-42- 9-2	96	87	34
S-42- 9-1	94	83	89
S-42-13-4	88	87	62
Average	96.29	89.00	69.30

The data in Table 6 do not indicate a close correlation between permeability in the vial test and germination in soil in the greenhouse. While no actual study of seed rotting or pre-emergence damping off was conducted the differences in germination of Ceresan-treated and non-treated seed indicates that some micro-organism or micro-organisms were responsible for pre-emergence mortality in a sporadic manner. Ceresan dusting of the seed provided some but apparently not complete protection against such organism or organisms. Jackobs (3) had recently demonstrated that *Pythium spp.* may cause sweet clover seed to rot before the hypocotol begins to elongate and that such rotting occurred at random. Accepting the assumption that pre-emergence mortality was of a random type in the test reported in Table 6, it is apparent that such sporadic mortality could disturb the correlation between permeability in the vial test and germination in the greenhouse soil. However, it is apparent from the data that unscarified seed of the highly permeable lines was capable of producing a high percentage emergence under greenhouse conditions.

In a study to compare the permeability in the vial test with that in soil under field conditions, twelve plants were selected the seed of which ranged between 58 to 100 per cent permeable in the vial test. Scarified and unscarified lots of seed of the Arctic variety were included as checks, the scarified seed having been obtained from a local seed-house. Open-pollinated seed of each of the selected plants and seed of the two check

lots was sown in copper screen troughs each about two feet long and $\frac{3}{4}$ inch deep. The mesh of the copper screen was fine enough to prevent the seeds passing through it. Four replicates of 125 seeds each were sown of each strain and check. After placing the seeds in the bottom of the troughs they were then filled with soil known to be free of sweet clover seed and were placed in the field with the top of the troughs flush with the soil surface. The strains and checks were randomized within the replicates.

At the time of seeding the field soil was very dry and, in order to provide relatively satisfactory and uniform moisture conditions, the test was watered with a garden sprinkler at planting time and again a few days later. Notes were taken four weeks after seeding and again eight weeks after seeding. The troughs were then carefully taken up, the bulk of the soil removed, and the ungerminated seed washed from the remaining soil.

The data obtained from this test are summarized in Table 7.

TABLE 7.—GERMINATION, PRE- AND POST-EMERGENCE MORTALITY AND STAND OF HEALTHY SEEDLINGS RESULTING FROM SEEDING UNSCARIFIED SEED OF PERMEABLE SEEDED PLANTS COMPARED TO THAT OF SEEDING SCARIFIED AND UNSCARIFIED ARCTIC UNDER FIELD CONDITIONS

Source of plant from which seed was used	Per cent of permeable seed in		4 weeks after seeding		
			% of seed sown resulting in		
	Field test at end of 8 weeks	Vial test	Dead seedlings prior to emergence	Dead emerged seedlings	Healthy emerged seedlings
407-2-3	98.0	100.0	44.8	29.2	24.0
407-42-20	97.6	100.0	31.0	30.8	35.8
407-49-3	100.0	100.0	49.4	37.8	12.8
407-49-7	89.8	100.0	28.6	41.4	19.8
407-20-4	99.2	98.0	23.2	33.0	43.0
407-34-1	98.6	98.0	28.8	47.0	22.8
407-42-36	96.8	90.0	39.6	23.2	34.0
407-42-27	90.0	84.0	38.6	31.2	20.2
407-2-13	88.2	78.0	27.4	44.2	16.6
407-20-20	98.0	80.0	39.8	16.0	42.2
407-17-18	74.8	64.0	16.6	11.4	46.8
407-26-27	65.2	58.0	23.2	16.8	25.2
Scar. Arctic	96.8	—	45.4	21.0	30.4
Unscar. Arctic	5.8	2.0	5.2	0.0	0.6

Comparing the second and third columns of Table 7 it is apparent that in general there is a close correspondence between permeability as determined in the vial test and in soil in the field. There is an unaccountable discrepancy between the two tests on seed of plant 407-20-20 but in other plants such differences as do appear may be due, in part, to the fact that the sample upon which permeability was determined in the field was ten times larger than the sample used in the vial test. In the field test the data presented on permeability also represent the germination. With this fact in mind it is clear that the seed which was shown to be highly permeable in the laboratory was highly viable. The unscarified seeds of the most highly permeable plants were fully the equal of well scarified commercial seed in ability to germinate.

The fourth column of Table 7 gives the percentage of seed sown which germinated but resulted in dead seedlings prior to emergence. The mortality before emergence was decidedly high but there is no evidence of any relationship between permeability and pre-emergence mortality. The mortality of seedlings arising from the unscarified seed of permeable seeded plants was, with one minor exception, lower than that of seedlings from scarified seed of the Arctic variety.

On the other hand post-emergence mortality as shown in column 5 was considerably higher in the case of most progenies of highly permeable plants than it was in the scarified Arctic; but again there was no apparent relationship between permeability and mortality.

As a consequence of pre- and post-emergence mortality at the end of four weeks the stand of healthy seedlings (per cent of seed sown resulting in healthy seedlings) was higher for five and lower for seven progenies of permeable seeded lines than it was for scarified Arctic. It has been pointed out that this mortality occurred haphazardly. Thus there is no relationship shown between permeability and stand four weeks after seeding within the group of permeable seeded lines or scarified Arctic but the stand obtained from unscarified Arctic was very much lower than in the other material and was definitely due to the low permeability.

Although irrelevant to the main topic of discussion it is expedient to point out that four weeks after seeding in general from 50 to 87 per cent of the seedlings had died prior to or after emergence. Data obtained eight weeks after seeding demonstrated that there had been further mortality between the end of the fourth and eighth week after seeding. In highly permeable material and in scarified Arctic the total pre- and post-emergence mortality ranged roughly between 70 to 90 per cent of the seed sown. These facts indicate the necessity of attempting to select for resistance to the disease organisms causing the pre- and post-emergence rotting. Jackobs (3) has shown that highly significant differences exist between the rotting of seed from different plants and thus it should be possible to select for resistance.

Nature of Permeability

Stevenson (8) described the occurrence of brownish sunken irregular shaped spots on the seed coat of seed of a number of highly permeable plants. He stated that "treatment of these seeds with osmic acid shows that the discolored areas coincide with the areas of absorption of water" and further that "permeable seed coats, however, were not confined alone to those seeds which possessed discolored areas".

From the first discovery of seeds having the spotted seed coats in the winter of 1935-36 no conscious effort has been made to select plants producing seed having this character. However, through the process of selecting the most highly permeable plants in the lines of highest average permeability unconscious selection has resulted for lines producing a very high proportion of spotted seed. All of the highly permeable lines now available have a high proportion of seed with the sunken brownish spots. This fact is evidence of the relationship of the spotting and permeability.

Further evidence of this relationship was secured from a study of open-pollinated lots of seed from twenty different plants the seed of which in the vial tests had ranged between 28 and 98 per cent permeability. Random samples of one hundred seeds were counted out from each of these plants, except in the case of plant 50-11 where only ninety-five seeds were available. Using a low power binocular each seed was examined carefully and segregated into one or other of the following classes: definitely spotted, indistinctly spotted, or not spotted. Following the separation into the three classes, the seeds of each class of each plant were given the regular permeability test. The results of this study are presented in Table 8.

TABLE 8.—OCCURRENCE OF SPOTS ON THE SEED COAT AND THEIR RELATION TO PERMEABILITY OF THE SEED

Source of seed Blk. 407	Per cent permeability of bulk sample of seed	Percentage of seed			Per cent of seed permeable		
		Definitely spotted	Indistinctly spotted	Not spotted	Definitely spotted	Indistinctly spotted	Not spotted
50-1	98	98.0	2.0	0.0	100.0	100.0	0.0
28-4	94	72.0	23.0	5.0	100.0	82.6	40.0
25-35	94	84.0	11.0	5.0	100.0	63.6	20.0
18-43	92	78.0	16.0	6.0	100.0	81.2	33.3
25-2	88	71.0	23.0	6.0	100.0	52.2	16.7
18-6	84	59.0	31.0	10.0	100.0	87.1	0.0
50-4	82	88.0	7.0	5.0	94.3	14.3	0.0
18-8	80	66.0	26.0	8.0	100.0	84.6	0.0
28-9	80	70.0	20.0	10.0	94.3	70.0	30.0
50-27	78	75.0	16.0	9.0	96.0	50.0	0.0
25-7	76	81.0	15.0	4.0	100.0	93.3	0.0
18-1	74	79.0	17.0	4.0	100.0	82.3	0.0
18-21	72	67.0	21.0	12.0	100.0	71.4	25.0
25-32	72	79.0	14.0	7.0	100.0	64.3	0.0
28-14	68	69.0	20.0	11.0	95.6	65.0	36.3
18-36	66	51.0	31.0	18.0	100.0	87.1	11.1
50-25	64	35.0	16.0	49.0	71.4	25.0	4.1
50-11	60	50.5	22.1	25.3	70.0	23.8	8.2
50-34	58	63.0	9.0	28.0	93.7	11.1	10.7
50-6	28	37.0	22.0	41.0	75.7	54.5	14.6
Total No. seeds		1372	361.0	262.0	1319	239.0	31.0
Ave. %		68.8	18.1	13.1	96.1	66.2	11.8

The plants are listed in Table 8 in descending order of permeability as determined in the original permeability test. It is seen in column 3 of Table 8 that, although the percentage of definitely spotted seeds was somewhat variable, there was a general relationship between the proportion of such spotted seeds and the permeability of the bulk lot of seed from which the definitely spotted seeds were segregated. From column 5 it is evident that the percentage of non-spotted seeds bears an inverse relationship to the percentage permeability. The percentage of seeds classed as indistinctly spotted varied within the range 2 to 31 per cent and there was no apparent relationship between the frequency of their occurrence and permeability.

The spotted seeds were highly permeable as is shown in column 6. From twelve of the twenty plants the spotted seeds were completely permeable and from five plants they were about 95 per cent permeable, while on three plants the spotted seed ranged between 70 and 75 per cent permeable. As an average 96.1 per cent of the 1372 definitely spotted seeds tested were permeable. The indistinctly spotted seeds were highly variable in permeability ranging between 11.1 and 100 per cent but averaging 66.2 per cent. Non-spotted seed of eight of the twenty plants was completely impermeable but non-spotted seed of the remaining plants ranged between 4.1 and 40.0 per cent permeable. In general the non-spotted seeds lacked permeability.

The relationship between spotting and permeability was further demonstrated by estimating the permeability from an examination of seed for spotting and correlating the estimated with the determined permeability. An F_2 population of a cross between a permeable and non-permeable line was used for this study. In estimating permeability one worker counted out a sample of fifty seeds and determined the number of seeds which were distinctly spotted, indistinctly spotted and not spotted. Assuming that the distinctly spotted seeds would be 100 per cent permeable, the indistinctly spotted 50 per cent permeable, and the non-spotted seeds impermeable, an estimate of permeability was arrived at. Completely independently another worker determined the permeability by the regular vial test method. The correlation surface for estimated and actual permeability is presented in Table 9.

TABLE 9.—CORRELATION SURFACE OF DETERMINED PERMEABILITY WITH ESTIMATED PERMEABILITY BASED ON THE DEGREE OF SEED COAT SPOTTING

Estimated permeability classes (%)	Determined permeability classes									
	0-9	10-19	20-29	30-39	40-49	50-59	60-69	70-79	80-89	90-100
90-100	—	—	—	—	—	—	—	4	13	18
80-89	—	—	—	—	—	2	3	15	23	4
70-79	—	—	—	1	2	8	16	12	8	1
60-69	—	—	2	6	3	14	12	13	6	—
50-59	—	2	12	8	9	8	12	3	—	—
40-49	—	1	8	10	8	8	3	1	1	1
30-39	1	—	4	13	12	5	4	1	—	—
20-29	4	10	13	5	4	2	—	—	—	—
10-19	11	9	7	3	1	—	—	—	—	—
0- 9	567	51	14	2	1	—	—	—	—	—

$r = +.96$

For $N = \alpha$ $P = .05$ $r = 0.62$

$N = \alpha$ $P = .01$ $r = .081$

From Table 9 it is clearly shown that there is a very high correlation between estimated and determined permeability. From the evidence of this high correlation and the data presented in Table 8 it is clearly demonstrated that the permeability of the material now being worked with is dependent upon the occurrence of the brownish coloured spots on the seed coat.

The nature of the spotting has not been studied beyond that described by Stevenson (8). He pointed out that in the spotted discolored areas on the seed coat "the cuticle is frequently broken; the matrix is thinner than

normal. The light line is very indistinct. The Malphegean cells are shorter and clefts are apparent between them and the osteosclerid cells are mostly collapsed". He pointed out that in some sections through the spotted discolored areas "bits of tissue resembling fungus mycelia were observed" but added that if such were the case "the fungus in no way interfered with growth, flowering or seed setting of the plants".

Although no intensive study of the spotted seeds has been made to determine whether or not they were bacterial or fungus lesions, it can be stated that if the spotting is due to disease such disease has no other effect. The plants from which spotted seeds are secured are normal as far as can be observed in vegetative and reproductive structure.

Preliminary Studies on Inheritance of Permeability

In the field nursery in the summer of 1939 crosses were made between highly permeable line S-30-11-$\bar{1}$-4-3-2 and the Alpha variety (4), a strain low in free coumarin (9), a late flowering *M. alba* designated S-268, and the Redfield Yellow variety of *M. suaueolens*. Since the Alpha and low free coumarin characters are inherited as simple recessives (5) (2), use of these varieties as female parents permitted the distinguishing of crosses from selfs in the F_1. In the cross involving Redfield Yellow the F_1 had cream coloured flowers (6) and could be distinguished from selfs. In crosses in which S-268 was one parent no criteria could be used to separate crosses from selfs.

The F_1 generation was grown in the greenhouse where, by rolling the flowers between the thumb and forefingers, a fair amount of selfed seed was obtained. However, the quantity was not deemed sufficient to permit a permeability test to be made. Actually such a test could have been conducted and the seedlings of these seeds which germinated could have been transplanted to soil and the impermeable seeds scarified. However, close examination of the seed obtained from the F_1 plants failed to reveal any spotting which may be taken as evidence that they were impermeable. This conclusion is supported by the fact that the F_2 data presented below show permeability to be recessive.

The frequency distribution for the F_2 generation derived from each cross is presented in Table 10.

It is obvious from Table 10 that high permeability is recessive. The number of factors controlling permeability is, however, difficult if not impossible to determine from the data. The fact that in three of the four crosses the F_2 populations were approximately equally distributed among each of the permeability classes from the 30 to 39 per cent class upward is evidence of complex inheritance. In the case of the cross involving the low coumarin strain, however, there is evidence of a bi-modal distribution which indicates a monohybrid ratio. An effort to interpret the data on the basis of one or two factors failed, however, to disclose any genetic ratio which could be applied to all four crosses. It is therefore concluded, on the basis of data presented in Table 10, that the permeable seeded character is inherited in a complex manner. This conclusion is further supported by the fact shown in earlier tables that attainment of highly permeable lines has been a slow process. If the character was simply inherited this would not have been the case.

TABLE 10.—FREQUENCY DISTRIBUTION FOR PERMEABILITY OF THE F_2 OF CROSSES BETWEEN A HIGHLY PERMEABLE SEEDED LINE (S-30-11-1-4-3-2) AND IMPERMEABLE SEEDED VARIETIES

Parent or F_2	No. of plants in % permeability class										Ave. % permeability
	0-9	10-19	20-29	30-39	40-49	50-59	60-69	70-79	80-89	90-100	
	Alpha (P_1) × highly permeable (P_2)										
P_1	13	6	5	—	—	—	—	—	—	—	11.17
P_2	—	—	—	1	—	4	12	9	1	—	65.98
F_2	98	27	17	8	4	6	5	3	5	1	17.78
	Low coumarin (P_1) × highly permeable (P_2)										
P_2	1	—	—	1	2	10	13	5	—	—	58.88
F_2	159	24	3	2	1	5	7	12	21	14	24.06
	S-268 (P_1) × highly permeable (P_2)										
P_1	26	1	—	—	—	—	—	—	—	—	4.87
P_2	—	—	—	—	—	6	6	—	—	—	59.50
F_2	261	9	17	6	1	3	4	2	2	1	9.17
	Redfield yellow (P_1) × highly permeable (P_2)										
P_1	18	2	—	—	—	—	—	—	—	—	5.50
P_2	—	—	—	1	3	6	9	5	3	—	63.02
F_2	59	17	9	4	4	3	—	—	—	—	12.62

From the breeding standpoint it is of interest to note that in the F_2 of three of the four crosses some plants were secured which were more highly permeable than the most permeable seeded plants of permeable seeded parent. Since the populations of the F_2 generations were considerably larger than the selfed progenies of the parents it cannot be definitely stated whether or not this represented transgressive segregation. However, it has already been pointed out that some of most permeable seeded lines now available are derivatives of the superior plants in these F_2 populations, which fact would support the theory that transgressive segregation had been obtained in the F_2 generation.

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SUMMARY

Seed coat permeability of single plants has been determined by placing 50 hand-collected, mature, open-pollinated, unscarified seeds in a glass vial in water for five days.

Permeability as determined by the vial test was found to correspond closely with permeability as determined by the official germination test. In the case of highly permeable seeded plants the permeability values corresponded closely to the official germination values.

One strain (S-28-5b) has been continuously selected for high seed coat permeability through two open and five successive self-pollinated generations. Generally modal class values for permeability and the lower limits of distribution were found to become progressively higher and there was a narrowing of the range of distribution with each advance in generation.

During selection through one open- and five self-pollinated generations of another strain (S-30-11), improvement for high permeability was less pronounced and more erratic than for strain S-28-5b. However, by S_5 the distribution was mainly confined to the moderately high to high permeability value.

In the F_2 of a cross of S-30-11 $\times$ Pioneer only about 30 per cent of population had a permeability of 21 per cent or higher. Selection for high permeability resulted in F_3 and F_4 in which over 90 per cent of the population was distributed in the 90 to 100 per cent permeability class.

The most permeable seeded line in the nursery had an average permeability of 98.2 per cent. In addition six lines ranged between 93.0 and 95.4 per cent average permeability. In comparison the average permeability of 114 presumably scarified commercial lots submitted for official germination test was found to be 88.8 per cent and unscarified seed of 98 Arctic and Pioneer plants was 3.6 per cent.

Germination of unscarified seed of the permeable seeded lines in soil in the greenhouse was good; but, due to sporadic pre-emergence mortality apparently caused by disease, an accurate comparison between permeability in the vial test and in greenhouse soil was not secured.

Seed of twelve plants displaying a considerable range in permeability gave essentially the same permeability values in the vial test as when sown in soil under field conditions.

Under field conditions from 16.6 to 49.4 per cent of the seed sown either rotted or the seedlings died before emergence. In addition from 11.4 to 47.0 per cent of the seed sown resulted in emerged seedlings which died within four weeks of the date of seeding. There was no relationship between the degree of natural permeability of the seed and seed or seedling mortality.

Permeability was shown to be associated with the occurrence of sunken, brownish, irregular shaped spots on the seed coat. As an average, seeds having such spots were 96.1 per cent permeable whereas not spotted seeds from the same plants were 11.8 per cent permeable. Seeds on which spots were only partially developed had an average of 66.2 per cent permeability. No evidence was obtained as to the nature of the seed spots. If caused by disease there was no other apparent effect on the plants.

Data were presented on the permeability of the F_2 progenies of the permeable seeded strain S-30-11 crossed with Alpha, Pioneer, and Redfield Yellow Varieties and with S-268 *M. alba*. A high proportion (75 per cent to 90 per cent) of the F_2 population fell with the range of 0 to 30 per cent permeability and the balance of the populations in three of the four crosses was distributed approximately equally over the balance of the permeability range. In the one cross there was an indication of a bi-modal distribution. It was concluded that the inheritance was complex and the number of factors involved could not be ascertained. A few F_2 segregates exceeded the upper limits of permeability distribution of the permeable seeded parent.

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PLANT TISSUE TESTING

III. EFFECT OF FERTILIZER APPLICATIONS[1]

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Over a period of three years, plant tissue testing by the method developed by Thornton *et al.* (7) was carried out on crops grown on the fertility plots of the Division of Chemistry, Science Service, Ottawa. In a previous publication (1), a description of the experimental area, crops grown, fertilizer treatments and procedure followed was given, together with the results obtained during the 1943 season. This area is referred to as area No. 1 and has been in continuous cultivation for many years. A second area (No. 2) which had been in sod for at least 15 years was brought under cultivation in 1945 and its level of fertility was found to be considerably higher than that of area No. 1. At this time the original experiment was enlarged so that the effect of different rates of fertilizer application on the composition of plant tissue on both areas could be studied. The basic NPK fertilizer treatment was equivalent to an application of 4-8-10 fertilizer at the rate of 1000 lb. per acre. Treatments such as 3NPK, N3PK and NP3K containing three times the amount of N, P and K, respectively applied in the basic treatment, were included.

NITRATE TESTS ON AREA No. 1

On area 1, crops have always responded to applications of nitrogen but not of phosphorus and potassium. While some variation in tissue test results between plants was observed during the first year of the experiment, a relationship was indicated between results for nitrates and crop yields. A summary of results obtained over a three-year period is presented in Table 1, where tissue tests for nitrates are compared with relative crop yields, the yield of the untreated plot being taken as 100 per cent. Three crops—tomatoes, potatoes and corn—were grown, and five treatments, viz. check, PK, NP, NK and NPK, were compared. The tissue tests were made in each case during the month of July and the values given represent the averages for the treatments.

An examination of the data in Table 1 shows that there was some variation from year to year and also between crops. The tests on the corn crop in 1943 were low, regardless of treatment, although there was a definite increase in yield where the fertilizer treatment contained nitrogen. The tests on potatoes in 1944 were high on all treatments and the yield response to nitrogen was not marked. In general, however, the amounts of nitrates found in the tissues and the yields of the various crops were higher where nitrogen was applied. This was most marked in 1943 and least in 1944. The best agreement between tests and yields was obtained with tomatoes, the poorest with corn.

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TABLE 1.—TISSUE TESTS FOR NITRATES AND RELATIVE CROP YIELDS, 1943-44-45

Crop	Treatment	1943		1944		1945	
		Avg. test*	Rel. yield	Avg. test	Rel. yield	Avg. test	Rel. yield
Tomatoes	Check	L	100	M	100	VL	100
	PK	L	99	LM	94	VL	114
	NP	H	242	H	125	MH	200
	NK	M	278	MH	127	M	153
	NPK	H	287	M	110	MH	198
Potatoes	Check	L	100	VH	100	M	100
	PK	VL	104	H	118	L	106
	NP	VH	217	VH	130	VH	173
	NK	H	216	VH	126	H	124
	NPK	H	221	VH	119	H	128
Corn	Check	VL	100	M	100	L	100
	PK	VL	105	LM	94	L	133
	NP	L	246	MH	134	MH	165
	NK	VL	233	MH	99	H	188
	NPK	L	241	M	89	MH	188

*VL = very low.
L = low.
M = medium.
H = high.
VH = very high.

QUANTITATIVE DETERMINATIONS

Tissue tests with crops grown on this and other locations showed that, in many cases, results by the method used were always very high, regardless of fertilizer treatment. This was found to be particularly true in measuring potassium in the potato stalk. Where all tests were thus classified, it was impossible to distinguish between the actual amounts present, and seasonal changes or the effect of varying rates of application could not be shown. In order to do this, some quantitative determinations appeared to be necessary. Samples of fresh plant tissue were extracted in a Waring blender with a sodium acetate solution to which activated carbon had been added (5). The amounts of nitrate, phosphate and potassium were determined quantitatively in these extracts by standard methods.

Results are presented in Table 2 to show seasonal trends in the concentration of nitrates, phosphates and potassium, as well as the effect of varying rates of fertilizer application on the amounts of these constituents in potato stems. The values show p.p.m. N as NO_3, p.p.m. P as PO_4 and p.p.m. K found in the sodium acetate extracts. These agree fairly well with results obtained in Virginia by Carolus and Woltz (3) who extracted potato plant tissue by grinding with 2 per cent acetic acid solution in a mortar and obtained values of approximately 500 to 1500 p.p.m. N as NO_3, 60 to 250 p.p.m. soluble P and 3000 to 7500 p.p.m. K.

On area 1, a light sandy loam that had been in continuous cultivation for a number of years, the concentration of nitrates in the plant tended to decrease during the season. On area 2, a light sandy loam that had been in sod for about 15 years but was ploughed and cultivated the fall previous to this experiment, the concentration of nitrates was greatest at the second

TABLE 2.—EFFECT OF SEASONAL CHANGES AND RATES OF APPLICATION ON NITRATES, PHOSPHATES AND POTASSIUM IN POTATO STEMS

		(As p.p.m. fresh tissue)			
		Treatment	1st sampling	2nd sampling	3rd sampling
Nitrates	Area 1	Check	1200	775	775
		NPK	900	625	350
		3NPK	3000	1975	1900
Nitrates	Area 2	Check	1350	2050	1625
		NPK	1475	2300	1675
		3NPK	1900	3000	2100
Phosphates	Area 1	Check	85	160	125
		NPK	55	120	50
		N2PK	70	115	50
Phosphates	Area 2	Check	85	105	70
		NPK	100	60	60
		N3PK	100	100	75
Potassium	Area 1	Check	6000	4750	3650
		NPK	6850	6250	5300
		NP2K	8700	7700	7850
Potassium	Area 2	Check	5500	4950	2650
		NPK	6400	6000	4350
		NP3K	7750	7200	5250

sampling date. This may have been due to the presence of a considerable amount of undecomposed grass roots early in the season, since subsequent results on both areas with potatoes, corn and oats, showed a tendency for nitrate concentration in the plant to become less as the season advanced.

The phosphate concentration of the plants on area 1 was greatest at the second sampling date, but no definite trend was observed on area 2. It was observed in this study that, while the phosphate concentration tended to decrease toward the end of the season, it was also somewhat influenced by the amount of nitrates present. Frequently when the concentration of nitrates was low, the phosphates tended to accumulate and, when nitrates were present in relatively large amounts, the concentration of phosphates decreased. This inverse relationship between nitrates and phosphates had been observed by other workers (6).

The concentration of potassium in the plants from both areas was greatest at the first sampling date and decreased throughout the season. This was the general trend with crops grown on these areas, though some exceptions were observed.

The application of nitrogen in the fertilizer has generally resulted in an increase in the nitrate concentration of the plant. This is shown in the table by the results on area 2 and with the higher rate of application on area 1. The lower concentration of nitrates in the plants grown on the NPK treatment, compared with those from the untreated plots, may have been due to the greater uptake of this nutrient with the improved plant growth.

The fertilizer application of phosphorus did not always result in an increased amount of phosphate in the tissues according to the figures in Table 2. This has been a general observation in this study with other crops also and may be related to the nitrate concentration as indicated above. The results given for potassium indicate quite clearly that the addition of this nutrient to the soil definitely increased its concentration in the potato plant tissue and results with other plants showed a similar trend.

COMPARISON OF RESULTS WITH YIELDS

Throughout the investigation on the use of plant tissue tests, an attempt has been made to see whether some relationship might be found between test results and crop yields. As illustrative of the values obtained, figures are presented in Table 3 showing yields and tissue test results for nitrates, phosphates and potassium at two sampling dates on potato plants from two treatments on the two areas previously described. In the case of both treatments, the yields were much lower on the plots of area 1 than on those of area 2. In comparing the tissue test results for the check plots, it is seen that the nitrates were considerably lower in the plants from area 1 toward the end of the season, and the phosphates were considerably higher. The amounts of potassium were also found to be somewhat higher in the plants from area 1. In this comparison, the difference in yield might be considered associated with the lower nitrate concentration, particularly since crops were shown to respond to applications of nitrogen on area 1.

In the 3NPK treatments, a considerable amount of nitrogen was applied to the soil which, as shown above, usually increased the values of the nitrate tests. The results in Table 3 show that, on both areas at the first sampling date, nitrates in the potato plants from these treatments were increased above those found in the plants grown on the check plots and, toward the end of the season, nitrates in both cases were at approximately the same level. There were no marked differences in the phosphate and potassium levels between the two areas where 3NPK was applied, although potassium was present in slightly greater amounts in the plants of area 1 when the third set of samples was taken. In general, it would appear that there were no great differences in the concentrations of nitrates, phosphates and potassium in potato plants grown on plots receiving 3NPK treatments on two areas; nevertheless, the yield on area 2 was double that on area 1.

TABLE 3.—COMPARISON OF TISSUE TEST VALUES AND YIELDS

Treatment	Nitrates		Phosphates		Potassium		Yield
	1st sampling	3rd sampling	1st sampling	3rd sampling	1st sampling	3rd sampling	
	p.p.m.N	p.p.m.N	p.p.m.P	p.p.m.P	p.p.m.K	p.p.m.K	bu/ac
Check—Area 1	1200	775	85	125	6000	3650	95
Check—Area 2	1350	1625	85	70	5500	2650	285
3NPK—Area 1	3000	1900	65	45	6750	5000	117
3NPK—Area 2	1900	2100	80	50	6750	4200	232

DISCUSSION

The application of plant tissue tests to problems of soil fertility has become rather widespread during the past few years and many workers have found them to be quite helpful in a large number of cases. In the work which has been discussed in this paper, results over a period of three years showed some relationship between tissue tests for nitrates and crop yields. These results, however, varied with the crop as well as from year to year.

No satisfactory relationship between crop yields and tissue tests for phosphates and potassium was found. These results appear to agree with those found by other workers. In a recent paper, Wolf and Ichisaka (8) state: "Because of variability of phosphorus and potassium in the plant, due to other causes than the availability of these elements in the soil, the usefulness of plant analysis as a practical guide to fertilization of spinach is limited. Nitrogen analysis of the plant seems to have more value."

In cases where the tissue tests for a series of treatments were always very high, it was found expedient to make quantitative measurements in order to distinguish between amounts present. This was done by extracting fresh tissue with a sodium acetate solution. From the results obtained, it was found that the concentration of nitrates and potassium tended to decrease during the season. Trends in phosphate concentration were not so definite. Increasing the application of nitrogen and potassium in the fertilizer brought about increases in the concentration of the nutrients in potato plant stems, but increased amounts of phosphorus applied to the soil did not always have a corresponding effect on plant phosphates.

Similar results were obtained in another investigation (4) in which analyses of dried leaves from corn and tomato plants grown on the same areas were made. The total amount of nitrogen in the leaves was increased when high rates of a nitrogenous fertilizer were used and the leaf content of potassium was increased whenever potassium was applied to the soil. On the other hand, levels of phosphorus in the dried leaves were not affected by phosphatic fertilizer applications.

In considering results from the areas of widely different fertility levels as indicated by crop yields, it was observed that quantities of nitrates, phosphates and potassium extracted from plants grown with the same fertilizer treatments were quite similar. From the tissue test results, it might be concluded that the nutrient supply for the plants on both areas was quite satisfactory. In view of the fact that the yield from one area was double that from the other, it would appear that some factor not measured by these tests affected the growth and production of the crops. Plants were apparently getting satisfactory quantities of the three major nutrient elements without making optimum growth.

SUMMARY

Studies of the use of plant tissue tests, using crops grown on the fertility plots of the Division of Chemistry, Science Service, Ottawa, have been carried out over a period of several years. Thornton's rapid test method, and extraction of fresh plant tissue with sodium acetate solution have been used.

Over a period of three years, on an area where crops responded to nitrogen fertilization, some agreement between crop yields and tissue test results for nitrates was observed.

Analysis of sodium acetate extracts of fresh potato stems showed that the concentration of nitrates and potassium usually decreased as the season advanced. The concentration of phosphates tended to be at lower levels late in the growth period.

The amounts of nitrates and potassium found in the plant tissues were usually increased when these nutrients were supplied in the fertilizer. The concentration of plant phosphates was not similarly affected by the addition of phosphorus to the soil.

Frequently when the nitrate concentration was increased, that of phosphate decreased, and when the amount of nitrates showed a decrease, that of phosphates showed an increase.

It was observed that plants grown on the same fertilizer treatment on different areas could have approximately the same concentration of nitrates, phosphates and potassium in their tissues, but the yield from one area could be double that from the other.

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